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Species distribution model for the Roan antelope (*Hippotragus equinus*) in the West African savanna

MASTER'S THESIS

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Declaration

I hereby declare that I have done this thesis entitled 'Species distribution model for the Roan antelope (*Hippotragus equinus*) in the West African savanna' independently, all texts in this thesis are original, and all the sources have been quoted and acknowledged by means of complete references and according to Citation rules of the FTA.

In Prague 18/08/2023

BSc. Thalia Mathilde Pelegrin

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Abstract

With constantly developing technologies, conservation of species has increasingly become a multidisciplinary approach, often using both on-the-field and computer-based methods to expand our understanding of different aspects such as behaviour, distribution, threats faced, and more. Species distribution modelling is one of these techniques that has become frequently used as it enables conservationists to comprehend where species occur, what drives them, and how this may change in the future. Within this discipline, several different methods have been developed, allowing the use of various predictors from a wide array of global databases. In this thesis, the distribution of the Roan antelope was studied in Niokolo-Koba National Park situated in Senegal, using various environmental variables. These were chosen based on knowledge of species ecology and included elevation, slope, distance to river and marshes, normalized difference vegetation index and its standard deviation, above ground woody biomass, mean annual temperature, temperature seasonality, maximum temperature of the warmest month, annual precipitation, and precipitation seasonality. Species data was collected from camera traps located within the centre of the park and used to create various species distribution models. Statistical evaluation and selection of these models was then performed to determine the most robust model with a good fit. This model (containing above ground woody biomass as a predictor of occupancy) was then used to extrapolate the probability of presence of Roan both in the park and a smaller area of interest within its borders. The model outputs predicted a high probability of Roan presence almost everywhere across the park, consistent with results expected from a generalist antelope with a high level of adaptability for a broad range of ecological conditions. However, in the absence of data available from the borders of the park, where other factors such as anthropogenic influence may affect predictions, precautions must be made when interpreting model results. Future studies to further increase our knowledge on Roan distribution would benefit from including more data sources of different factors, comprising ideally of multi-seasonal data, as well as expanding the area of study to include a wider range of habitats.

Key words: Environmental modelling, Large herbivore distribution, Roan antelope, Senegal, Species Distribution Modelling

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1. Introduction

Ecosystems are complex environments made up of a wide variety of interactions between organisms and their abiotic surroundings (Beale et al. 2013). Each function efficiently in a continuously moving equilibrium that enables diversity and evolution to take place. In order to understand how that happens, it is crucial to comprehend the ecosystem itself, what lives in it, the interactions that take place in it, and the optimal conditions required for it to thrive. This can mean looking at factors at different levels, from the microscopic interactions of bacteria in the soil to the larger organisms that shape the physical environment through disturbances, such as large herbivores (Treydte et al. 2009).

The Roan antelope (*Hippotragus equinus*), hereinafter referred to as Roan, is one of these large herbivores that is widely spread across the African continent (Gonçalves et al. 2021). At a species level it is considered least concern by the IUCN SSC Antelope Specialist Group (2017), although their population trend is decreasing. However, the Roan distribution is fragmented mainly due to increased human population and urbanization, and local populations in Southern Africa are currently endangered due to livestock encroachment (Castello 2016). Additionally, although they have been extensively studied in Southern Africa, there is a paucity in data on the Roan in North West Africa, including in Niokolo-Koba National Park (NKNP) in Senegal and little is known about their distribution, what pressures they face, what interactions and factors affect their populations as well as their habitat requirements.

One way to look at these interactions and better understand a specific ecosystem is by using spatial occupancy. With advancing technologies, including mapping techniques such as Geographic Information Systems (GIS) and spatially explicit data collecting methods like camera trapping, or telemetry collars, there is the possibility of understanding where species are present and absent. Moreover, using methods such as camera trapping enables us to gain further knowledge on the daily patterns of activity of species, and better understand their circadian rhythm, whether it differs across populations, habitats or seasons, which is a crucial aspect of movement ecology to understand and take into account when looking at distribution (Owen-Smith & Goodall 2014; Blank & Li 2022). Furthermore, with the increased development of these techniques there is also the possibility of investigating which external factors, whether they be environmental or anthropogenic, and depending on data available, affect a species presence in a specific area, and how this may change in the future.

Understanding and looking at the distribution of a species is particularly important as it can inform us on the environment that is most suitable for it and can help us predict where we may find a species, or where they could survive if needed. Additionally, with the current climate change situation we are facing and the uncertainty of future suitable habitats, it has become particularly important to look at wildlife spatial distribution in order to help make long-term conservation objectives when it comes to protecting a specific species or ecosystem.

This thesis focuses on understanding the different drivers of large herbivore distribution and uses this alongside existing knowledge on the species to study the current distribution of Roan in NKNP. In order to do so, camera trap data from the dry season of 2021 paired with various environmental variables are compiled to create species distribution models (SDMs), which are then evaluated and discussed with prospects of future studies.

2. Aims of the thesis

The objective of this thesis was to expand the understanding of distribution of the Roan antelope (*Hippotragus equinus*) in the context of West African savanna ecosystems, including existing pressures over West African protected areas, specifically Niokolo-Koba National Park (NKNP).

The specific aims of this thesis were 1) to select and evaluate drivers of Roan distribution to be used as variables for prediction, 2) to use species distribution models (SDMs) to create an occupancy model and predict Roan distribution through extrapolation over an area of interest (AOI) and the entirety of NKNP, and 3) to assess the circadian activity pattern of Roan to understand behaviour in the given ecological context of the NKNP.

3. Theoretical background

3.1. Drivers of distribution of large herbivores

Distribution and densities of large herbivores are variable across different ecosystems and are often described as being affected by a multitude of factors that can be spatial and temporal in nature (Bailey et al. 1996; Van Beest et al. 2011). Additionally, these factors can be biotic or abiotic, as well as naturally occurring or exacerbated anthropogenically (Young et al. 2020). They are often not mutually exclusive, instead creating a complex interconnected web of push and pull factors, which all play a role in driving the habitat use and distribution of herbivores (see Figure 1). Understanding these factors and the pressure they exert on different herbivores is crucial to form an idea of herbivore movement and their distribution. This, in turn, is important knowledge required to properly inform the current and future conservation measures of different species, their populations, and the ecosystems they reside in.

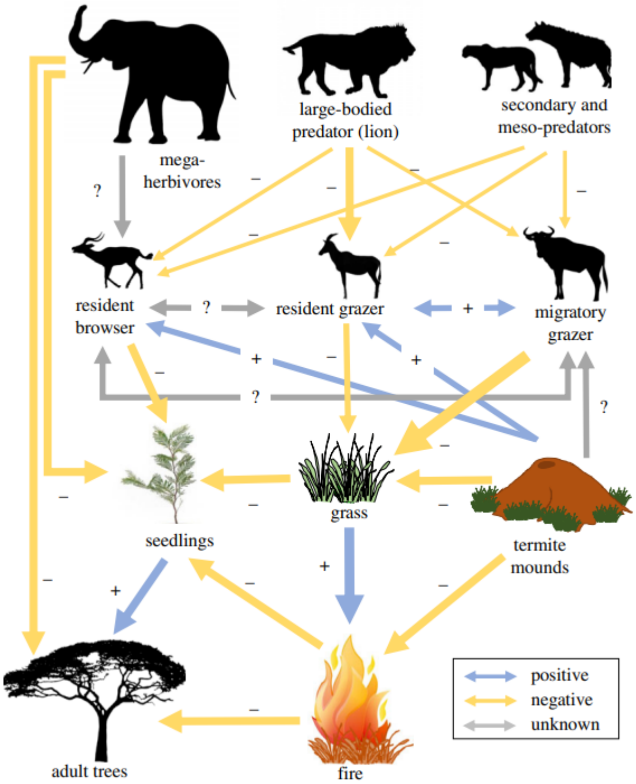


Figure 1: Framework created by Anderson et al. (2016) explaining trophic interactions as an example of different drivers of herbivore distribution

3.1.1. Biotic factors

Ecosystems are in a continuous shifting state, with different pressures changing their composition. However, there is often an underlying fluid equilibrium, due to different elements more or less balancing each other out. Biotic factors, which encompass all living things, are one type of these elements, abiotic factors being another. There are several different biotic factors, all of which interact with each other as well as with abiotic factors, and together they act as drivers of species distribution. For large herbivores such as Roan, the biotic factors that drive their distribution include but are not limited to: predation, food availability and habitat heterogeneity, competition, and human activity.

Predation

Predation is an interaction whereby one organism kills and consumes another. It is a driver of distribution of large herbivores because as prey species, they may actively adjust and avoid areas with high or frequent levels of predation events in order to reduce predator encounters (Laundré 2010). Predation affects large herbivores in both a direct top-down effect via depredation, as well as through the creation of a ‘landscape of fear’, which will determine when and how intensely herbivores will forage and is dependent on recent predation events in a particular area (Anderson et al. 2016). However, since predation risk and foraging availability are the principal opposing forces that act as top-down and bottom-up drivers of habitat selectivity, respectively, predation on its own does not explain the distribution of herbivores (Sinclair et al. 2003). Therefore, it is linked to multiple other factors, including food availability, which in turn is connected to the species biology of both the predator and the prey.

Predators are limited by their feeding strategy in terms of the habitat they are found in, and can successfully hunt in. For example, cheetahs (*Acinonyx jubatus*) are typically restricted to large open grassland areas due to their hunting strategy relying predominantly on their short bursts of linear speed (Jeo et al. 2018). Whereas lions (*Panthera leo*) can adopt both a stalking or ambush strategy, partially dependent on their pride dynamics, enabling them to inhabit more cryptic heterogenous landscapes (Loarie et al. 2013). Nevertheless, these strategies are not only limited by habitat, but also by the response of their prey to the imminent threat of predation (Thaker et al. 2011; Martin & Owen-Smith 2016). Herbivores have two principal responses to predators: fleeing; or freezing and hiding, which is strongly linked to both their feeding strategy (browsers or grazers) and their body size (Burkepile et al. 2013). In general, larger herbivores (which are often gregarious) have lower predation risks per capita than smaller ones, but require higher food abundance, which results in them actively occupying or travelling through areas of higher predation risk than smaller herbivores, who actively seek out higher food quality over abundance (Anderson et al. 2016). However, Riginos and Grace (2008), found this was not always the case, when a large herbivore (Giraffe, *Giraffa camelopardalis*) actively selected a more open ‘safer’ habitat with less food abundance, than an enclosed one which had higher predation risk from lions, whilst a smaller herbivore (Steenbok, *Raphicerus campestris*) selected the closed habitat with higher food quality and predation risk. This was presumed to be due to the differences in the response of the two species, giraffes in general fleeing, which is easier to do in an open area, whereas steenboks freeze and hide, which is beneficial in a more cryptic habitat (Wirsing et al. 2010).

In addition to the selection of habitat as an a priori modification in response to perceived predation risk, there is also the reactive response or adjustment after a predator encounter that will affect habitat selectivity of herbivores (Courbin et al. 2016). This is once again dependent on the feeding strategy of the prey. In a paper by Martin and Owen-Smith (2016), the immediate and 24-hour response of both plains zebras (*Equus quagga*) and blue wildebeest (*Connochaetus taurinus*) to lion encounters was studied in Kruger national park, South Africa. The plains zebras, which are described as inhabiting a wider range of habitats, fled the encounter areas and were found in subsequently lower food quality habitats, whereas blue wildebeest being more selective of a particular rarer habitat type, were less likely to relocate following an encounter. The cost of relocation was thus dependent on the feeding strategy of the prey species and influenced the blue wildebeest more strongly due to their narrower habitat requirements. A final factor that has also been studied to influence habitat selectivity of larger herbivores in relation to predation, is the daily pattern of activities of both prey and predator species (Owen-Smith 2019). Lions, being the principal cause of mortality of ungulates in Africa, are often described as predominantly nocturnal hunters (Yiu et al. 2022), and in response to that, most prey species, which are predominantly diurnal, will prioritise foraging activities during the day and actively avoid areas of higher predation risk at night (such as waterholes), where they are more vulnerable (Burkepile et al. 2013).

Food availability and habitat heterogeneity

As previously mentioned, food availability is one of the main drivers alongside predation risk affecting habitat selection of large herbivores. These two factors trade-off against each other in complex ways and are often impacted by what aspect of food availability is most important to a species: the quality or quantity of forage. Additionally, these drivers may shift in importance throughout seasons, or an individual's lifetime. Food availability aspect is highly correlated to body size and the feeding strategy of herbivores: grazers or browsers, ruminants or non-ruminants (Fritz & Loison 2006; Burkepile et al. 2013). The general consensus is that large herbivores often favour food abundance or quantity over quality, as opposed to smaller herbivores, thus leading larger herbivores to be distributed in a wider range of habitat types (Du Toit & Owen-Smith 1989; Groom & Harris 2010). However, it is important to note that this trend is apparent only for ruminants, since smaller ruminants are restricted to certain habitats whereas similarly weighted non-ruminants (which also have a higher tolerance to varied food quality levels) are more evenly distributed (Cromsigt et al. 2009).

Studying food availability in large ecosystems such as African savannas can prove difficult, especially when looking at a multi-species approach. Nevertheless, studies have found using Normalized Difference Vegetation Index (NDVI) as a measure of plant productivity and thus quality and abundance, has been successful in determining distribution of large herbivores (Pettorelli et al. 2011; Muposhi et al. 2016). Using NDVI as one of their environmental factors, a study by Bhola et al. (2012) showed that larger herbivores were associated with high values of NDVI, signifying high levels of 'greenness' of vegetation, to which the main habitat type was grass that was both tall and dense. This also connects with the species biology of larger herbivores, which are frequently gregarious in nature, and thus require large areas of vegetation suited to their diet and survival (Fryxell 1991). However, although NDVI is an extremely useful tool, on its own, it is often not enough to account for how food availability acts as a pressure of large herbivore distribution. Habitat heterogeneity, or in other words the variability of habitat types in a given area, is a closely linked factor of food availability and has become an increasingly important aspect of managing protected areas, in order to maintain the diversity of ungulates and other species (Muposhi et al. 2016). It is crucial to consider habitat heterogeneity in smaller areas, to counteract fragmentation, and where the possibility of migration is limited and the benefits of buffering in larger areas is not present (Anderson et al. 2016). Additionally, it is also an important factor to consider when speaking of ecotone species (such as the Roan), that tend to thrive in diverse habitats of different levels of food quality.

Competition

In African savannas, competition is widespread for the simple reason that the continent has the highest diversity of ungulates, and thus large herbivores (Fritz & Loison 2006). This and the fact that as herbivores, they will primarily occupy similar niches increases the presence of competition and its effect on the distribution of these herbivores. There are three general assumptions to take into account when trying to understand competition and determine whether it is present. These assumptions apply both to intra-specific and inter-specific competition, but when observing it as a driver of distribution of a species, studies have principally taken into account competition between species (Sinclair 1985). The assumptions are that in order for competition to exist, there needs to be an overlap in habitat, an overlap in resource consumption within that habitat, and the resource itself is limited (Traill 2004). If these are present, it is likely competition is occurring, and additionally, likely that this is influencing distribution of at least one of the species (usually the one that is outcompeted).

South Africa has been a pioneer in both historic exploitation of large herbivores, and more recently become a strong advocate towards their conservation. This has increased the amount of research done in trying to determine the factors that have led to drastic population declines of certain species, such as the Roan (Harrington et al. 1999). Inter-specific competition has been identified as a factor that has an effect on declines in herbivore populations, as well as a driver of their distribution (Wilson & Hirst 1977). This inter-specific competition was studied to have a direct impact, by means of landscape-use changes or resource-use shifts to avoid competition for resources of several large herbivores (Mariotti et al. 2020). However, there was also an indirect impact identified. Harrington et al. (1999) studied the causes of decline of the Roan in Kruger national park, South Africa, after their population numbers decreased from approximately 450 animals to 45 remaining individuals. The results showed that the higher number of artificial waterholes added to habitats predominantly used by Roan, increased competition by attracting other herbivores to the area. In addition to the direct competition for forage near the newly placed waterholes, the herbivores also changed the surrounding landscapes, strongly diminishing grass cover used by Roan to hide their calves. This increased the mortality rate, particularly due to the influx of herbivores to the area attracting higher numbers of predators. Overall, competition is a factor that affects the distribution of herbivores, however, it is important to note that it can be enhanced by human activity either indirectly as mentioned above through the change of land management, as well as directly via competition between wildlife and livestock, which has become a more common issue (Bhola et al. 2012).

Human activity

In recent years, the steady growth of human population has increasingly created man-made pressures on natural environments. Whether it is through activities linked to land-use change such as agricultural development, pastoralism, and mining, or illegal activities such as poaching and bushmeat hunting, these events have undeniable effects on the distribution of large herbivores, and as a result on the rest of the ecosystem they live in (Watson et al. 2014; Ripple et al. 2015). These pressures have been observed affecting populations of large herbivores within protected areas, often causing niche compression, increased inter-specific competition, and an overall imbalance in ecosystem functions (Bhola et al. 2012; Tucker et al. 2018).

A long-term study in Kafue National park in Zambia, researched the effects of different anthropogenic pressures on 10 species of large herbivores including the Roan (Vinks et al. 2020). Results clearly showed an increase in density of herbivores with proximity to human activity (villages and roads), which seems counterintuitive. A proposed explanation for this was that the location of these settlements and infrastructures was in a highly productive part of the park, consequently attracting herbivores despite the increased pressure of habitat degradation and poaching. Additionally, it is important to consider that where there was the highest density of humans was also where touristic activities were prominent, so a stronger anti-poaching presence was expected, thus reduced poaching pressure.

Kimanzi et al. (2015), studied the distribution of snares in relation to other ecologically important factors affecting both Roan and other herbivore species distribution, in Ruma national park in Kenya. Snares are a particularly cruel method of poaching, which consists of attaching a loop of wire between two trees or structures and once the animal goes through, it tightens until the individual is trapped. This can cause deep lacerations, as well as a slow painful death through dehydration. Unfortunately, it is one of the most prominent tools in African wildlife poaching due to its effectiveness, minimal effort level, and low cost, leading to several hundred snares being placed in a small area. The results of the study showed that these 'hotspots' of snares occurred in the vicinity of water, salt and foraging resources, where high density of herbivores is expected. Interestingly, they did not coincide with areas Roan were found in. Nevertheless, the drastic losses of more than 80% of Roan within 30 years within Ruma national park have been identified as predominantly caused by snaring incidents (Kimanzi et al. 2015). These declines in populations as a result of human activity inevitably impact the distribution of these species. However, it is often difficult to support direct relationships of anthropogenic drivers to distribution as they themselves are variable and affected by other factors such as environmental conditions.

3.1.2. Abiotic factors

Although biotic factors have been intensely studied in relation to the distribution of large herbivores, these studies often look at biotic factors in combination with abiotic factors which are permanently interlinked (Anderson et al. 2016). These abiotic factors often exert different pressures on biotic factors, and their resulting effect on distribution. They can be quick-acting with immediate responses, as well as change gradually over a long period of time. In African savannas the most prominent abiotic changes studied are: fire, water availability, and, more recently, climate change.

Fire

African savannas are strongly influenced by fire regimens, both natural and man-made. This is chiefly due to their large biomass storage of flammable vegetation, particularly in the dry season. In liaison with this, fires are often used as a method of controlling ecological diversity, particularly in protected areas. However, there are various existing fire management techniques with different goals, some which can be detrimental to the long-term biodiversity of an area (Nieman et al. 2021). Fire exerts bottom-up control on large herbivore distribution principally by affecting the forage quality and quantity available (Owen-Smith et al. 2020; Young et al. 2020). This, in hand with the top-down control exerted by predation, presents a trade-off in habitat selection and utilisation for different species. This trade-off is dependent on other variables such as body mass and dietary requirement, as well as anti-predatory strategies employed by the herbivores and results in an intricate complex web of factors determining habitat selection in African savannas (Burkepile et al. 2013).

The general consensus on the effects of fire on large herbivore distribution is that the increase in young, highly nutritional biomass following a fire acts a ‘magnet’, essentially attracting animals to recently burned areas (Archibald et al. 2005; Klop et al. 2007; Anderson et al. 2016). Additionally, this is closely linked to an observation by Klop et al. (2007), demonstrating that the time period elapsed after a fire was an important factor in the determination of ungulate presence in a burned area, with results showing preference for recently/newly burnt areas when regrowth would be most abundant. Nevertheless, it is essential to understand other drivers of species distribution and their strength when studying the effects of fire, as it does not only bring new growth, but also an increased likeliness of competition (both intra- and inter-specific) and predation in the area (Harrington et al. 1999).

Water availability

Water is an essential resource required for the survival of all animals including large herbivores (Alpert 2005). However, certain species have specific adaptations enabling them to be less water-dependent, thus permitting them to live in more arid conditions. This can be beneficial as there tends to be less competitive pressure in these areas, however, the majority of large herbivores are considered on some level water-dependent.

African savannas tend to have very drastic differences in water availability throughout seasons and years, resulting in significant losses to animal lives via droughts and their impacts on forage (Kay 1997). Additionally, the frequency of drought events on a continental scale has gradually increased, as well as the duration of events (Masih et al. 2014). This has led to artificial water sources being put in place in numerous national parks as a management technique, especially when large amounts and variety of herbivores are present (Epaphras et al. 2007; Hayward & Hayward 2012). Their emplacement enables an effective reduction in the extent of detrimental effects seasonal rainfall variability has on the ecosystem and the species within them by essentially providing year-round access to surface water. This not only has important impacts throughout the year, but between years as well, particularly when there are scarce natural resources.

A study by Smit et al. (2007) in Kruger National Park observed grazers associating more with artificial waterholes, whereas browsers and mixed feeders associated instead with main rivers. A possible reason described is that there is a higher water content in browsing material rather than in grasses, particularly during the dry season, equating to a lack of sufficient water acquired by grazers through their food, requiring them to be more dependent on permanent water resources (Redfern et al. 2003). Additionally, geology was also an underlying factor, where all herbivores favoured water sources on nutrient rich soils where they had to travel less far from the water in order to find good quality forage. In this study, Roan being a selective grazer occurred at the highest densities around artificial waterholes rather than rivers. However, a previous study by Harrington et al. (1999) in Kruger National Park, contrastingly found that artificial waterholes increased foraging competition and predation risk to Roan, thereby pushing them away from these areas. Furthermore, it has also been proposed that providing year-round surface water in abundance may have detrimental effects such as homogenization of landscapes, as well as reduction of herbivore diversity, in addition with other unknown and unprecedented changes linked to climate change (Chamaillé-Jammes et al. 2007).

Climate change

Animal evolution enables adaptations to occur under changing pressures from their environments. However, this is a long-term process encompassing many aspects such as their species biology, genetics, plasticity, as well as their habitat requirements. Climate change, currently exacerbated by the Anthropocene, is a much quicker process whose timeline often prevents adequate adaptations, potentially leading to decreased diversity and increased extinctions. On a global scale, a study by Baisero et al. (2020) looked at the effects of changing climate on the habitat availability of mammals under different climatic scenarios. Their results portrayed a decline on all continents with a global 5-16% decrease in habitat, and up to 25% on the African continent. This indicated both the urgency and importance of addressing land-use change in sub-Saharan Africa, particularly with thought towards future climatic possibilities.

Climate change is an increasingly discussed topic in liaison with land-use change and is specifically linked to the direct consequences of increased habitat fragmentation resulting from unmanaged land-use change (Wu et al. 2016). It is particularly prominent on the African continent primarily due to increased population growth leading to augmented demands of land. This is strongly connected to how climate change acts as a driver of distribution on large herbivores because not only does it isolate populations, preventing and changing their natural distribution, it also causes niche compression, behavioural changes, and can fundamentally change the biology of the species (Fuller et al. 2016). Climate change directly affects animals, via changes in temperature, precipitation, and frequency of extreme events (see Figure 2). This is exceptionally important to consider in large herbivores, since temperature and precipitation will have an undeniable effect on their thermoregulatory properties and water requirements, respectively. However, it is imperative to understand that differences in large herbivore species biology play an equally important role in determining the effect of climate change on their distribution.

It has been stated that extreme droughts linked to future climatic changes are predicted to decrease the diversity of larger herbivores which are (frequently more) water-dependent in favour of smaller ones that are more water-independent (Veldhuis et al. 2019). There are certain exceptions to this, particularly in herbivores well-adapted to arid environments. Nevertheless, it is understood that phenotypic plasticity is a crucial aspect of understanding how species and their distribution may be affected by changing habitats as result of climate change (Fuller et al. 2016). Furthermore, this is not only the case for climate change, but all other factors that have the potential to affect distribution of species. Di Marco et al. (2014), have demonstrated that species biology is a crucial aspect of understanding the effects of different factors that drive distribution of large herbivores, including climate change. Therefore, the next chapter of this literature review will address the species biology of the Roan, in order to expand on the knowledge available, and enable the selection of both biotic and abiotic factors to be studied and their effect on the distribution of Roan in NKNP.

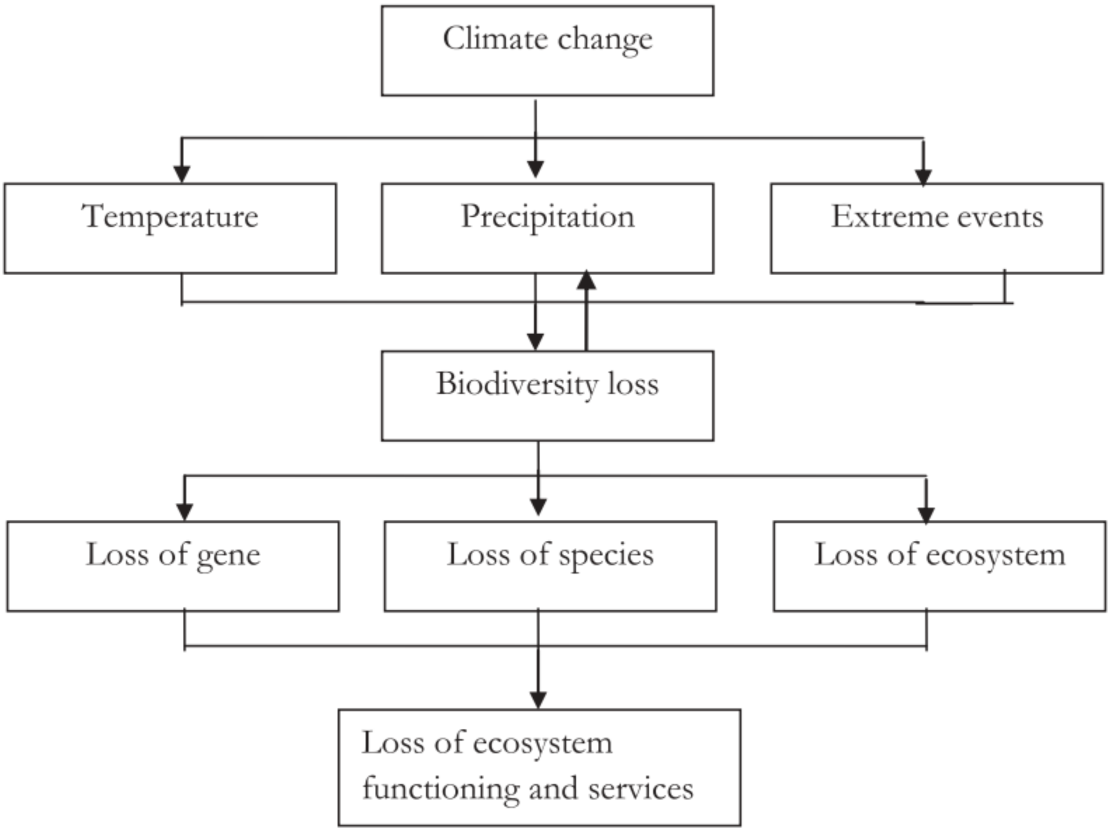


Figure 2: Diagram about climate change, its parameters, and their impact on biodiversity, created by Sintayehu (2018)

3.2. Roan antelope

3.2.1. Taxonomy and conservation status

The Roan antelope is a species of even-toed ungulates belonging to the tribe Hippotragini (also known as horse-like antelopes) within the family Bovidae. The Hippotragini tribe is comprised of antelopes described as having barrel-shaped bodies, long ears, striped or marked faces and evenly ringed horns, and there are six extant species within three genera: *Oryx*, *Addax*, and *Hippotragus*, the last of which includes the Roan (Estes & Kingdon 2015). The Roan is related closely enough to the Sable antelope (*Hippotragus niger*) to produce viable hybrid offspring. However, its nearest relative is the now extinct Bluebuck (*Hippotragus leucophaeus*) despite it physically being smaller and Roan being more similarly attributed to the Sable (Hassanin et al. 2012).

The species was first described in 1803, but the taxonomy to this day remains uncertain. In 1971 the Roan was classified morphologically into six subspecies, in accordance with its geographic range (Ansell 1971). Using mitochondrial DNA and microsatellite genotyping, Alpers et al. (2004) later suggested that only the subspecies proposed from West Africa was genetically distinct (*Hippotragus equinus koba*) from the remaining East, Central and Southern African lineage. However, another approach has been to recognise five subspecies using the biological species concepts (Frost 2014). The systematics of this species is still ambiguous and disputed due to the existence of different approaches to taxonomy, such as the biological and phylogenetic species concept (Frost 2014; Castello 2016), and limited geographical genetic sampling often leading to inaccurate descriptions of species divergence (Gonçalves et al. 2021). The most up-to-date phylogeographic study on Roan has proposed that the West African lineage of the species is the most ancient, before expanding into the rest of sub-Saharan Africa (Gonçalves et al. 2021). Nevertheless, for the focus of this thesis which puts attention solely on the population found in NKNP, thus only the West African subspecies (*Hippotragus equinus koba*) is considered, the unclarity of taxonomy is not of great importance.

Regardless of the present uncertainty on the division into subspecies, the species as a whole is currently listed as ‘least concern’, under the International Union for Conservation of Nature (IUCN) Redlist criteria, justified by the species widespread range and a large percentage being in protected areas. Nevertheless, a decreasing population trend has been identified and if continued may change the Roan to a more threatened conservation status (IUCN SSC Antelope Specialist Group 2017). Additionally, it is important to note that the majority of studies on the Roan have focal areas in Southern and East Africa (mainly in Kruger national park in South Africa and the Serengeti national park in Tanzania) (Hofer et al. 1996; Harrington et al. 1999), and much remains unknown of the conservation status of populations in West Africa.

3.2.2. Morphology

Roan are described as the second largest antelope in the world, after the members of the *Taurotragus* genus, which solely comprises of the common and giant eland (*Taurotragus oryx* and *Taurotragus derbianus,* respectively) (Furstenberg 2011; Frost 2014; Kingdon 2015). However, this has also been disputed due to the nondescriptive word ‘largest’ which can describe height as well as weight, and male Greater Kudus (*Tragelaphus strepsiceros*) can reach similar measurements (Owen-Smith 2013). Nevertheless, they are ultimately considered large herbivores, weighing up to 270kg with females being slightly smaller at around 230kg (Furstenberg 2011, Castello 2016). There is minimal sexual dimorphism aside from a slight difference in size. Horns are present in both sexes and are annulated in an even manner with only the tips being smooth, note that they are slenderer in females (Chardonnet & Crosmary 2013). Another defining trait are their large protuberant ears extending away from their head and ending with reddish fur, which can be up to 25-30 cm in length (Furstenberg 2011). Like most Hippotragini members, they have characteristic facial markings with high contrast which diminishes as they get older, the darker coloured fur often becoming grey or white (Chardonnet & Crosmary 2013). Their short dorsal mane is often lightly coloured with pale brown-greyish hair, however, ones in West Africa most commonly have a reddish tinge to them (see Figure 3).

Figure 3:Sub-adult Roan in Bandia reserve, Senegal (Photo credit: T.Pelegrin)

3.2.3. Distribution range

Historically, the Roan has been defined as having a widely spread sub-Saharan distribution range across the African continent, which is an accurate description of their current range, as can be seen on Figure 4 (Frost 2014; Castello 2016; IUCN SSC Antelope Specialist Group 2017). However, when the range is studied on a smaller scale, it is described as fragmented and heterogenous (Alpers et al. 2004; Gonçalves et al. 2021). Their range often overlaps with protected areas as well as areas surrounding these which have low densities of human population (East 1999). Southern populations have been highly studied in the past, particularly in South Africa, and were observed to be declining rapidly and losing much of their historic range until they became preserved under intensive management in private game ranches and national parks (Harrington et al. 1999; Furstenberg 2011). Nowadays, their population numbers are still low and they are considered one of the rarest antelope in Southern Africa. Populations persist in the majority of their native range in West Africa, although they have become regionally extinct in The Gambia (Castello 2016). Moreover, the patchiness of these populations in this region has not been determined, and thus their least concern status may deteriorate, especially with growing human populations further diminishing their numbers through land-use change, poaching, and other anthropogenic factors (East 1999; Chardonnay & Crosmary 2013; Havemann et al. 2016).

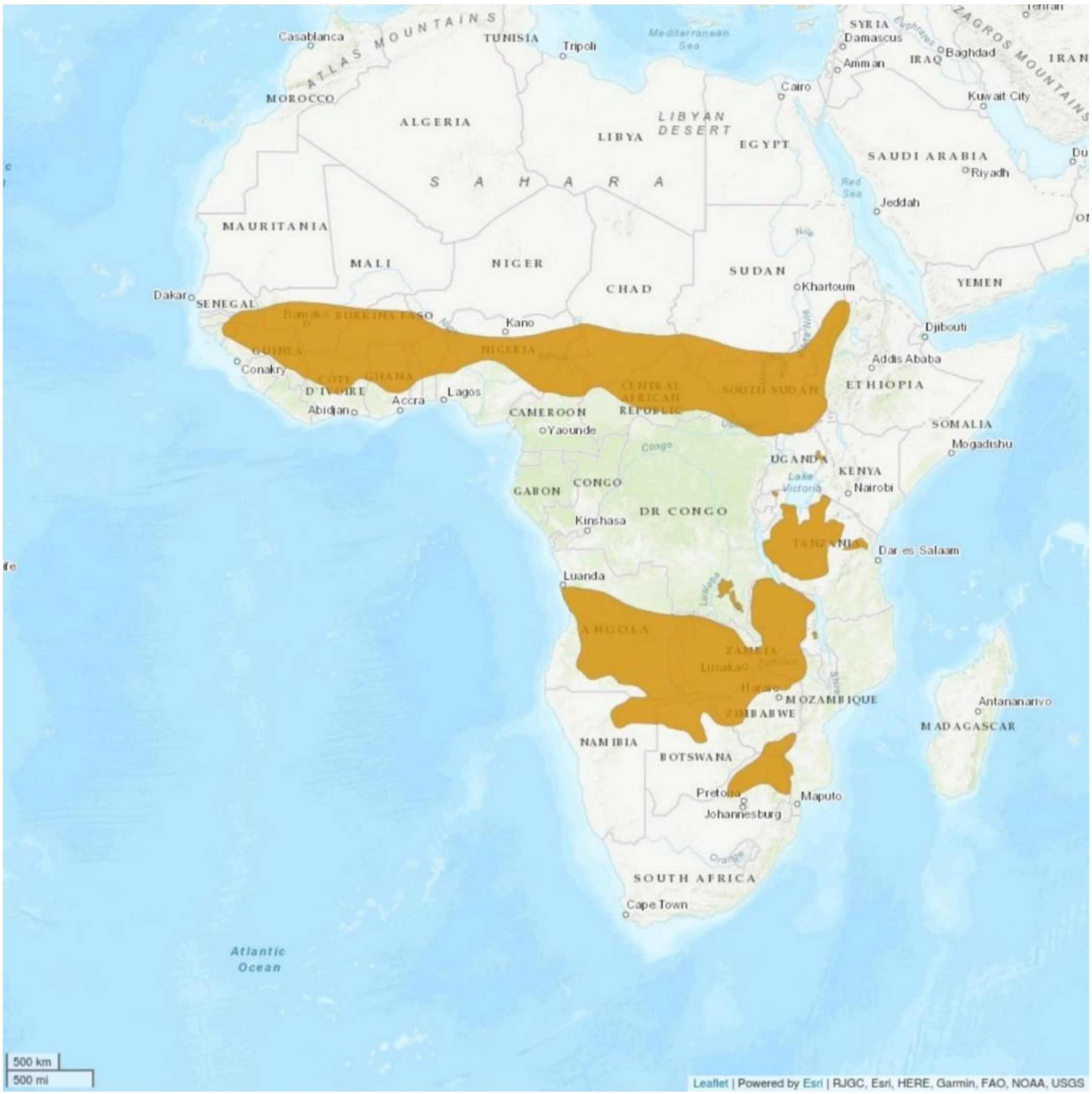


Figure 4:Distribution range of the Roan on a continental scale (IUCN SSC Antelope Specialist Group 2017)

3.2.4. Population size and dynamics

Although the population trend of the Roan has been labelled as decreasing by the IUCN SSC Antelope Specialist Group (2017), their current numbers remain largely unknown with the last population estimate ranging from 40,000 to 76,000 individuals (East 1999). This is outdated, and at the time only 30% of Roan were determined to have stable or increasing populations. These have since deteriorated further, particularly in Southern

Africa, with the exception of populations found within private reserves (Dörgeloh et al. 1996). However, despite a clear lack of data and studies in West Africa (Havemann et al. 2016), both on the species in general and their abundance, multiple authors have described populations as stable (Codron et al. 2009, Havemann et al. 2016). This assessment may be deceptive, as populations within national parks and other protected areas are described as either stable or decreasing (IUCN SSC Antelope Specialist Group 2017), but ones outside these areas are only decreasing. Additionally, their isolation from each other may lead to rapid declines in the near future (Havemann et al. 2016).

There are often two factors measured or assessed when looking at the population dynamics of a species: their fecundity, and their mortality rates and causes. Both of these aspects of the dynamic of a population are critical to comprehend the underlying factors affecting population size and status.

Fecundity: Roan are considered to be quite prolific breeders due to their peak potential productivity being at around 10 months per year, whilst their gestation is approximately nine months (Chardonnet & Crosmary 2013; Castello 2016). There is uncertainty surrounding the topic of their breeding season dependent on their geographic location. In general, studies from Southern Africa suggest they may breed all year round with no clearly defined breeding season (Furstenburg 2011; Castello 2016). Whereas in Central African Republic the breeding season is proposed in March and August, in Niger it is January to March, and in Rwanda April and September (Poche 1974; Delvingt & Lobão Tello 2004; Chardonnet & Crosmary 2013). Although the breeding time is different depending on locality, the calving usually coincides with the end of the wet seasons and the beginning of the dry seasons. Females become sexually mature and start reproducing at around two years of age with males of around six years old (Furstenberg 2011; Chardonnet & Crosmary 2013). They leave the herd to calve, often giving birth only to one offspring, though twins have been recorded (Poche 1974). Calves hide for four up to six weeks, joining the herd once they are able to keep up with the long distances travelled daily (Castello 2016; Havemann et al. 2016).

Mortality rate: Calves have the highest risk of mortality, with rates often exceeding 70% within their first year (Chardonnet & Crosmary 2013), depending on habitat and season as contributing factors. Due to calves being hiders, their camouflage consists of being odourless and remaining undetected in high grasses (Wilson & Hirst 1977; Havemann et al. 2016). However, if they are hiding in an unsuitable habitat, or one where other species of herbivores consume the grass that conceals them, they are highly likely to be predated on (Harrington et al. 1999). Additionally, season also influences predation risk on juveniles, since during the beginning of the wet season herds tend to be the most fragmented due to an abundance of food, often leaving the juveniles unattended and more vulnerable (Beudels et al. 1992).

3.2.5. Social behaviour

The general consensus on the social grouping status of the Roan is that they are a semi-gregarious species, with herds consisting of up to 20 individuals including one dominant breeding male, several reproductive females, and their offspring (Chardonnet & Crosmary 2013; Frost 2014; Havemann et al. 2016). This is dependent on season and food availability, as there have been vastly differing observations of groups numbering between 10 to 150 individuals (Kingdon 1982; Tyowua et al. 2012b). Additionally, there is dispute on their home range size and whether they overlap. The sizes of home ranges have been studied in several different areas with differing herd sizes and seems to be widely varying, anywhere between 200 and 10,000 hectares (Perrin & Taolo 1998; Havemann et al. 2016). It is thought by some that there is little to no overlap in home ranges (Furstenberg 2011; Frost 2014). However, studies have observed both the mixing of herds as well as higher tolerance of bulls towards each other during dry season (Allsop 1979; Cornelis et al. 2006). Nevertheless, whether there is overlap or not, it is clear that home ranges of Roan are maintained temporally, often throughout several generations, showing there is a trend of sedentarism within the species (Frost 2014; Castello 2016; Price 2016).

The area occupied by a herd is often distinguished through several visual and olfactory means, such as hoof digging and horning of the ground, dung heaps as well as gland secretions (Perrin & Taolo 1998). Although Roan males are not territorial in terms of permanent space, the dominant breeding male will maintain a ‘territory’ around his breeding herd and chase off any other adult males, including ones from his own herd when they are approximately two years old (Castello 2016). These will often join a bachelor herd until they reach sexual maturity at around six years old and will then try to push out a breeding male to take over a breeding herd (Chardonnet & Crosmary 2013). Similarly, there is also a hierarchy between females, and the actions of the dominant female dictate when and where the herd drinks and eats, and will be followed by everyone including the dominant male of the herd (Castello 2016). This can cause tension, particularly with female offspring of the dominant female, and can lead to a subdivision of the herd, which positively affects dispersal of the species (Chardonnet & Crosmary 2013).

Roan have been reported to be a particularly aggressive species, both intra- and inter-specifically, and will often charge and attempt to fight even when injured (Furstenberg 2011). Males frequently exhibit strength displays, particularly in bachelor herds, including chasing other males away, mock charging, and horn-sparring from a kneeling position as can be seen in Figure 5, which can lead to fatalities (Poche 1974; Allsop 1979; Frost 2014). Contrastingly, when it comes to their young, strong social bonds are observed. Juveniles often stay grouped together during the day in ‘nursing herds’ supervised by several adults, and when running away from something will follow just one female rather than separating each towards their own mother (Chardonnet & Crosmary 2013).

Figure 5: Two adult male Roan in a fighting display, one in the kneeling horn-sparring position, in Fathala wildlife reserve, Senegal (Photo credit: T.Pelegrin)

3.2.6. Habitat selection and diet

Understanding habitat selection is a key component in comprehending a species biology in terms of their diet and dispersal. Due to Roan being so widespread, it is particularly important to understand the type of habitat they are found in to properly inform conservation and management measures. Their habitat selection has been seen to vary, as would be expected for a species that spans across the African continent and differs both seasonally and with different populations (Dörgeloh 1998; Knoop & Owen-Smith 2006; IUCN SSC Antelope Specialist Group 2017). However, the general consensus is that they are found in a mix of habitat types ranging from partially wooded areas of the savanna during dry seasons, to tall grasses and more open areas during the wet season (Gureja & Owen-Smith 2002; Tyowua et al. 2012a; Chardonnet & Crosmary 2013; Kimanzi et al. 2013; Castello 2016; Gonçalves et al. 2021). Grass height ranges between 50 and 200cm, in other words tall enough to provide cover for their calves to hide (Chardonnet & Crosmary 2013; Havemann et al. 2016). They are considered by the majority of authors an ecotone species (Knoop & Owen-Smith 2006; Frost 2014; Havemann et al. 2016), meaning they are often found on borders of different ecosystems and in the presence of habitat variability (Kark 2013).

Surprisingly, as opposed to the majority of other grazers, studies have found no evidence of Roan being inclined to inhabit areas that have recently been touched by fire, where new growth is in abundance (Gureja & Owen-Smith 2002; Kimanzi et al. 2013; Frost 2014). This may be linked to the fact that they actively avoid areas where grazing competition is prominent (Heitkönig & Owen-Smith 1998; Mcloughin & Owen-Smith 2003; Knoop & Owen-Smith 2006; Frost 2014), which results in them being found in regions with nutrient-poor soil, and low forage quality (Heitkönig & Owen-Smith 1998; Chardonnet & Crosmary 2013). This is in line with other members of the Hippotragini tribe, such as the Addax (*Addax nasomaculatus*) or members of the *Oryx* genus, which are actively found in nutrient-deficient areas (Knight 2013; Newby 2013; Bro-Jørgensen 2016). However, as opposed to these species which are regarded as desert-like and that fulfil their water requirements via their food, Roan are described as water-dependent, and have been observed in lowlands such as floodplains near a water source (Kimanzi et al. 2013; Castello 2016; Gonçalves et al. 2021). Nevertheless, it remains unclear to what extent their dependency on surface water is, since they have equally been found further away than expected from a water resource for a water-dependent species and have been disputed as a water-independent species (Sinibaldi et al. 2004; Chardonnet & Crosmary 2013).

Roan are described as predominantly grazers, often found feeding in areas of intermediate-to-tall grass height, which is advantageous to them both for foraging with reduced competition and for hiding their calves (Knoop & Owen-Smith 2006; Chardonnet & Crosmary 2013). Contrastingly, the few studies from West and Central Africa have shown a distinct difference in browsing preference of Roan to ones in Southern and East Africa, distinguishing them as dietarily fluid and observed browsing more often, potentially due to reduced browse competition (Poche 1974; Chardonnet & Crosmary 2013). However, they are sometimes considered mixed feeders in Southern Africa, due to their change in foraging behaviour during dry season, often favouring browsing on dicots (Schuette et al. 1998; Perrin & Taolo 1999; Kimanzi et al. 2013). This strengthens the idea of their ecotone habitat selection, where they can get both grass and woody plant material in the same patch. Additionally, their diet has led authors to classify them as a habitat specialist species with a high sensitivity to habitat changes, especially ones exacerbated by anthropogenic means (Frost 2014; Knight et al. 2016). However, there is some debate on this as certain studies have described the diet of Roan as extremely selective, only feeding on a limited number of species (Perrin & Taolo 1999), whilst others have opposingly found their diet to comprise of more than 40 different species of graze and browse, and occasionally fruit parts of plants (Aremu 2004; Tyowua et al. 2013; Havemann et al. 2014).

3.2.7. Activity and dispersal

Activity patterns are often driven by several different factors, including but not limited to predation and its related avoidance behaviours, food availability, and species biology. Roan, being a large ruminating antelope, require long periods of inactivity and rest in order for proper digestion and nutritional accumulation, particularly when temperatures rise during the day, due to thermoregulatory constraints (Du Toit & Yetman 2005). Thus, they are predominantly diurnal organisms, their daily behaviour divided into two peaks of activity in the early morning until noon and in the evening once the temperatures have cooled down (Castello 2016). This enables them to ruminate during the hottest periods of the day, often under the shade of trees (Chardonnet & Crosmary 2013; personal observation). These activity patterns may vary during different seasons due to temperature changes and food availability and may affect the dispersal of Roan across their home range.

The movement and dispersal of species is inextricably linked to their activity patterns and daily requirements of both food and water. Additionally, external factors affect dispersal such as whether an organism is predominantly driven by avoidance of predators or by foraging requirements (Owen-Smith & Goodall 2014). Within their home range, which can widely vary is size from 2 to 100km^2 (Havemann et al. 2016), Roan have fluctuating patterns of dispersal. When food and water availability is optimal and competition minimal, they tend to stay in a particular patch for several days, leading a somewhat sedentary lifestyle before moving to another patch (Havemann et al. 2016; Price 2016). However, much like other members of the Hippotragini tribe, they are able to travel long distances daily if pressured by external factors (Kingdon 2015). Their ability to move further away from water sources than other water-dependent species and eat low quality forage enables them to travel up to 20 kilometres per day in search of food sources within their home range (Chardonnet & Crosmary 2013).

3.2.8. Values and threats

The value that we place in nature and on different organisms is tenuous and is frequently strongly linked to our increasingly high demands, mainly due to population growth. This has led to strong anthropogenic-caused changes that often destroy wildlife in order to supply a constantly growing need, or only conserve parts of it that are determined beneficial from a human perspective, and has thus led us to undervalue natural things on an intrinsic level (Batavia & Nelson 2017). For Roan, a species that is not particularly described as ‘charismatic’, the principal value attributed by humans is its trophy due to the impressive horn size, as well as the increasing rarity in Southern Africa where trophy hunting is most prominent (IUCN SSC Antelope Specialist Group 2017). Additionally, their locally endangered status may also be why they are considered valuable as a touristic attraction in those areas (Havemann et al. 2016). However, it is unfortunate that a tangible, often economical value must be placed in order for conservation measures to be put in place (Chardonnet & Crosmary 2013).

From a biological and ecological perspective, Roan are an important aspect of ecosystems, and their role as large herbivores in landscape dynamics should not be disregarded. As both an intermediate grazer and a prey species, they play an important role in habitat structure and food webs, respectively (Anderson et al. 2016). Additionally, as one of the only two extant species of the *Hippotragus* genus, they are an important part of historical conservation (Kingdon 2015). Unfortunately, these values have no economic metric, and are often disregarded as a result (Batavia & Nelson 2017), leading to a number of threats affecting the species, both anthropogenically centred and not.

There are often numerous factors interacting with each other on different levels that affect the state of ecosystems and the organisms that live within them. This is true for protected areas, that are considered refuges of wildlife, and are thus particularly vulnerable to a number of different threats, especially due to their increasing isolation (Newmark 2008; Scholte 2011). These threats then trickle down to affect the organisms within these ecosystems whether directly or indirectly and have been seen to cause dramatic decline in large mammal populations, particularly in West Africa where an 85% decline has been reported during a 35-year study by Craigie et al. (2010). The threats can be both anthropogenic or natural, although they are not mutually exclusive and often affect each other in a complex manner (Di Marco et al. 2014).

Roan, which previously were widespread, have already faced threats that have compelled them to being found almost exclusively in protected areas (IUCN SSC Antelope Specialist Group 2017). This threat stems predominantly from land-use changes caused by humans and the increasing demands of a growing human population (Brashares et al. 2001; Chardonnet & Crosmary 2013). These demands have not only limited Roan to isolated protected areas, but have also reduced the size of these areas usable to the species by means such as livestock encroachment, and illegal harvesting (Wittemyer et al. 2008; Scholte 2011). Additionally, the increased pressure of humans and their needs has led to high rates of poaching (Brashares et al. 2004; Kimanzi et al. 2015). These incidents are exacerbated in countries that are politically and economically unstable, such as many in West Africa, where drivers of poaching stem from inadequate protection due to lack of funds, the need for local people to survive and sustain themselves, and armed conflict (Craigie et al. 2010; Daskin & Pringle 2018).

Although the above-mentioned threats to Roan are directly connected to anthropogenic factors, this is not always the case. Many natural processes threaten Roan, such as predation, disease, and climate change. Nevertheless, this does not mean that there are no indirect pressures by humans on these threats that exacerbate their consequences. For example, Roan, being a prey species, have a constant 'threat' of being predated on, particularly by lions (*Panthera leo*), their principal predator (Harrington et al. 1999). However, in Kruger national park, South Africa, Roan populations dramatically decreased from 450 to 45 individuals in less than 10 years. This was attributed chiefly to the increased man-built waterholes in the more arid areas of the park, habitat selected predominantly by Roan. These waterholes increased the density of other grazers, thus increasing competition, reducing the ideal calf-hiding environment for Roan, and increasing the presence of predators drawn to the area by an abundance of prey (Mcloughin & Owen-Smith 2003). Another natural threat for Roan is diseases, which have been studied both in the wild and in captivity over time, portraying the species as sensitive to a wide array of pathogens (Wilson et al. 1974; Steyl et al. 2012; Kaiser et al. 2023). However, a study by Clegg et al. (2007) demonstrated just how strong of a threat this can be to Roan, especially to small isolated populations, when more than 40% of the Roan population in Malilangwe wildlife reserve, Zimbabwe was decimated by anthrax. The threat of diseases is likely to become more prominent and drastic with changing climate, particularly in tropical areas where infectious agents are likely to thrive (Ostfeld 2009; El-Sayed & Kamel 2020).

Climate change itself is a factor affecting many other pressures Roan face and is both difficult to understand, and difficult to predict in terms of its future effects. However, it is commonly understood that precipitation levels change as a result of climate change, and have already done so drastically in West Africa, potentially acting as a threat to the persistence of species, especially strongly water-dependent ones (Scholte 2011). Studies published before the 1970s in West Africa have shown high annual rainfall, but in 1970, Scholte et al. (2007) showed decreasing population trends of Roan and other species explained by drought events. From then, West African rainfall patterns have been described as below average when evaluated on a continental level (Scholte 2011). As our awareness about climate change and the potential threats it poses on both us and the environment has grown, it has led to an accumulation of studies and development of future prediction models, which, paired with an understanding of species distribution, can improve conservation measures.

3.3. Species distribution models (SDM)

3.3.1. Basic theory

What is it?

Species distribution modelling is an umbrella term used when quantifying correlations concerning the distribution of a species and environmental variables (Miller 2010). At its debut in the 1970s (Austin 1980), the purpose of SDM was to successfully model how different environmental variables affected species across space and time (Austin 2002). Nowadays, there are numerous other terminologies employed that each have different subtle connotations, such as ‘ecological niche modelling’, ‘habitat suitability modelling’ and ‘predictive mapping’ (Franklin 1995; Kimanzi et al. 2013; Tourinho & Vale 2023). When using varying terminology dependent on the study questions and data being used, it is important to keep in mind both the scale that is defined, ‘niche’ versus ‘habitat’, and the processes that are described, ‘mapping’ which is linked to a physical outcome versus ‘modelling’ which expresses the method applied (Miller 2010). Despite these different titles, they essentially have the same original goal, which is to determine how environmental variables shape species distribution, and thus answer a multitude of different questions related to species distribution. Furthermore, the application of SDM has grown exponentially, and they are now being used to inform and answer a wide variety of research questions. These include but are not limited to: conservation planning, indicating potential protected areas, monitoring of invasive alien species and rare/endemic species, and predicting effects of changing climate (Thuiller et al. 2008; Guisan et al. 2013; Schertler et al. 2020; Qazi et al. 2022).

Theory and process

The theoretical background applied to SDM is often said to be linked to the ecological niche concept (Guisan & Thuiller 2005). This is agreeable, since a basic understanding of the fundamental and realised niche of the target species will facilitate a basic comprehension of what factors may affect its distribution. However, certain problems arise from this, due to the different scales of interactions and behaviours linked to the niche concept, such as competition, mutualism, and even dispersal. Often, these processes cannot be understood collectively across the spatial-temporal scale of SDMs, thus distinctions tend to occur for better comprehension (Peterson et al. 2015). Therefore, although the niche concept remains a crucial aspect of SDM, the modelling is instead defined with the alternative term 'habitat' (Miller 2010). Thus, although recent advancement in modelling has increased to possibility of looking at the mechanistic interactions species have (Gobeyn et al. 2019; Tourinho & Vale 2023), the correlative approach focusing on an applied descriptive analysis of the response in terms of abundance or occurrence a species has to the environment is still prominent.

Once the scope of the study is defined and objectives are laid out, the process of SDM can be divided into four steps. These steps have been extensively reviewed in the past, enabling researchers to create SDMs with a reasonable level of understanding of the mechanics behind the models (Guisan & Zimmermann 2000; Elith & Leathwick 2009). A basic summary of these is presented below. The first step is correct data preparation, which includes both the species observation from a variety of sampling methods (whether this is abundance, or presence-absence data), and the environmental variables data at different gradients (direct, indirect, or resource). Once this is accomplished, model fitting is next, which is considered the most vital step. This is due to the fact that it not only incorporates a vigorous selection of models and their settings, but also requires an evaluation of the environmental variables, their potential multicollinearity, spatial and temporal autocorrelation, as well as the selection of threshold predictors if a binary prediction is desired. This is strongly linked to the third step which is model assessment (and is frequently performed simultaneously), as it includes assessing the importance of the different variables on distribution, both visually and statistically, and evaluating the credibility of the model using knowledge on the species biology and the environment. The final step to perform is predictions, which can be both in space and time. These include interpolations that look at the probability of the species occurring at unsampled sites within the same region and under similar environmental conditions, alongside extrapolations, which focus on probability of occurrence across time and space. However, although these predictions are useful to answer important questions in many different domains, it is necessary to consider the limitations of SDM and exercise caution when interpreting them.

Pros and cons

Modelling in any field is an extremely useful and powerful tool as it creates a simulation that enables the evaluation and better understanding of real-life situations. Additionally, it can be used for future predictions of complex systems and interactions, allowing for data-based decision making and development to take place (Guisan & Zimmermann 2000). However, like in any method, there are certain caveats to keep in mind. Below is a summary of the advantages and limitations that can be encountered when using SDM.

SDMs have the main advantage of predicting distribution of species across both space and time. This itself then trickles down to all the other benefits of species distribution modelling, which conclude in providing a framework that can be replicated across the globe to be enacted in conservation and management plans (Lissozsky et al. 2021). Another advantage of SDMs is their ability to look at a multitude of environmental variables simultaneously, which results in an integrated understanding of interactions between the species and the different factors, and an assessment of which ones may be the most crucial to take into account when managing distribution (Guisan & Zimmermann 2000; Miller 2010). Moreover, these factors can be looked at on different resolutions, allowing in some cases finer-scale predictions at high resolutions. However, it is important to acknowledge that different gradients of environmental factors may be present when evaluating species distribution at a specified scale (Franklin 1995). The transparency of SDMs in terms of their predictive power and limitations is itself another benefit, since despite those caveats they still provides an idea of more specific focus areas, which can then be employed in future surveying, thereby minimising the efforts required for success in terms of both fiscal expenses and time costs.

There are certain limitations associated with modelling species distribution, which should always be taken into account during the interpretation of results. The majority of them can be linked to the data that is input and used as a metric in the models, both for species and the environment. Firstly, data collection for both species occurrence and environmental factors has the potential to be time consuming and costly, thus a limitation particularly in hard-to-access areas. However, recent developments in census and monitoring (such as the use of camera traps) as well as satellite evolution has somehow reduced this limitation (Bowkett et al. 2007; Azzou et al. 2021). Nevertheless, despite these advances, data collection is not the only limitation found, and the data quality itself can be another limiting factor. This can be divided between species and environmental data. When speaking of species data, the main limitations that have been observed in studies using SDM is small sample size and sampling bias (Wisz et al. 2008; Fourcade et al. 2014). These biases can strongly affect predictions since the assumption of the models is that the species data input is representative of the species distribution, thus our validation and interpretation must be cautionary in liaison with our knowledge of the limits of our data. Furthermore, the environmental data that we input often limits the accuracy of the predictions as well, simply due to the fact that the resolution available may not be representative of the intricate complex interactions occurring (Miller 2010). Finally, it is important to acknowledge that predictions from SDM are likely to have errors occurring from these limitations in terms of both interpolation and extrapolation. Therefore, when interpreting results, high consideration should be placed on all aspects and steps of the modelling process. Despite the limitations discussed, species distribution modelling remains an extremely valuable tool in conservation, particularly with the uncertainty of future changes.

3.3.2. Types of SDMs

Methods of modelling species distribution

As SDMs have gained popularity in science, several methods have been developed in order to best suit different data and answer specific research questions. These methods can be based on statistical models, or they can use a machine learning algorithm. They each have their own set of assumptions and limitations which must be addressed. Table 1 provides a list of the main methods used for SDMs, and their advantages and limitations encountered when using them. This list is not exhaustive, and there are many other methods currently in use when looking at SDM. Additionally, it is not unusual to see a combination of different methods used that are evaluated separately and compared, in order to consider various levels of model viability and validation.

Table 1: Summary of main methods of SDM, their advantages and limitations

Method	Utilised by	Description	Advantages	Limitations
Generalised Linear Models	Guisan & Zimmermann 2000	Statistical models that use linear functions to look at relationships between species occurrence and environmental factors	Simple to manipulate and easy to interpret	Main assumption is a linear relationship between species occurrence and environmental data, thus subject to multicollinearity issues
Generalised Additive Models	Elith et al. 2006	Statistical models that are an extension of Generalised Linear Models, and are non-parametric in nature	Flexible and takes into account non-linear relationships	Computationally intensive, and additionally requires more data than Generalised Linear Models
Maximum Entropy	Phillips et al. 2006	Machine learning algorithm predicting species distribution under a set of limits	User-friendly, works well with both small sample sizes and non-linear relationships, and shows importance of different variables	Assumes equal distribution probability with the training and prediction, thus may overfit/estimate
Random Forest	Cutler et al. 2007	Machine learning algorithm predicting species distribution using decision trees	Useful if there is missing or outlier data, and shows importance of different variables	May overfit/estimate and is susceptible to selection of hyperparameters
Boosted Regression Trees	Yu et al. 2020	Machine learning algorithm predicting species distribution using a multitude of decision trees fitted to residual data	Works well with small sample sizes, shows importance of different variables and their interactions	May overfit/estimate and is susceptible to selection of hyperparameters

4. Methodology

4.1. Study area

Niokolo Koba national park is located in South East Senegal, on the border of Guinea (see Figure 6). It is the largest national park in Senegal, and it covers an area of 9130km^2. Originally, in 1926, it was a hunting reserve, however, its status changed into first a wildlife reserve in 1953, and then officially into a national park in 1954 (Renaud et al. 2006). It has been described as a biosphere reserve and a world heritage site in danger since 2007 (UNESCO 2023), and this status remains to this day both due to the increasing anthropogenic pressures faced with human population growth, as well as the resulting threats to several key species inhabiting the park.

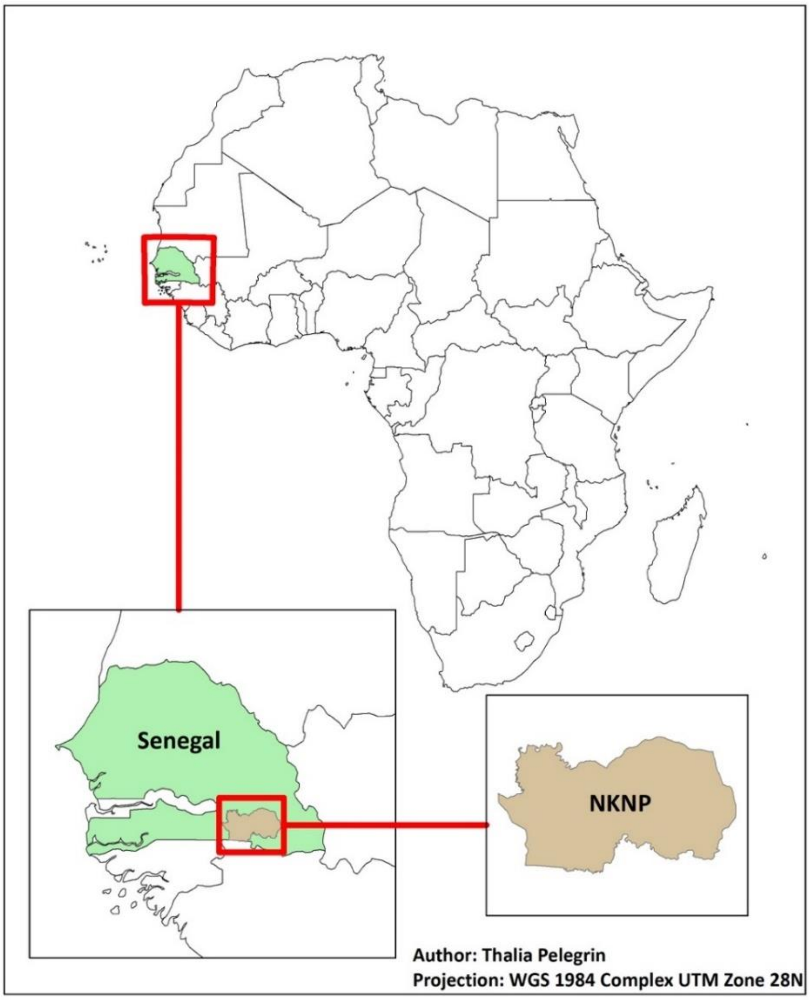


Figure 6: Position of the study area in relation to the African continent

The creation and maintenance of protected areas such as national parks like the NKNP are the principal device used to conserve African wildlife (Caro & Scholte 2007). As such, several measurable criteria are put in place to determine the emplacement of protected areas. These usually involve diversity of habitat types, endemic species, and/or species that are in danger of extinction. The NKNP is a refuge for regionally critically endangered species such as wild dogs (*Lycaon pictus*), West African lions (*Panthera leo*) and West African chimpanzees (*Pan troglodytes verus*), as well as the globally recognised critically endangered Western Derby eland (*Taurotragus derbianus derbianus*) (Rabeil et al. 2018). These species have not only sought refuge in NKNP, but are still under threat from direct factors such as poaching and livestock encroachment, as well as indirect factors such as decreased soil and water quality as a result of land-use changes principally via intensified agricultural practices (Henschel et al. 2014; Drouilly et al. 2021). Additionally, it is important to note that the national main road (N7), which travels from Dakar all the way to Mali, bisects the park increasing human presence and its subsequent impacts on wildlife. Therefore, simply understanding that the park is of crucial importance in terms of safeguarding wildlife is not enough, and detailed research on both the diversity and distribution of wildlife is equally imperative in order to properly manage and mitigate threats.

The rainfall patterns in the park are between 900 and 1200mm annually, in majority during the rainy season from June to October. However, owing to several hydrological sources: the Gambia River and the Niokolo-Koba stream, there are certain areas of the park with permanent water even during the dry season (Galat et al. 2015). These are both in the form of riverbanks, as well as several marshes that have a very distinct vegetation composition. These marches create a diverse habitat of gallery forests and open marshy meadows. The majority of other habitat types found within the park include grassy and scrub savannas, and dry forests (Dagorne et al. 2020). Additionally, although the elevation of the park is minimal (at a maximum of 311m above sea level), there are several plateaus which also create semi-isolated habitat types with distinctive vegetation. NKNP is very diverse in both flora and fauna, with up to 1500 species of plants, and more than 550 species of animal including 80 species of mammals (McGrew et al. 2014; Dagorne et al. 2020).

4.2. Camera trap data collection

During the months of March to June 2021, an evaluation of leopard (*Panthera pardus*) populations in NKNP by Panthera and the Direction des Parcs Nationaux du Sénégal (DPN) was undertaken using camera traps. The basis of this thesis used the bycatch of photos captured by the camera traps from this project containing Roan, in order to model their species distribution. The following is a summary of the project and camera trap details provided by the report created by Drouilly et al. (2021). The chief aim of the project was to carry out a rigorous observation of the fauna in the park, with special focus on the leopard and the previously mentioned regionally critically endangered species, to create a database that could be used in subsequent studies such as this thesis. Additionally, the project also aimed to estimate leopard populations, as well as identify threats to the wildlife within the park.

A total of 72 camera trap stations were created with the majority equipped with two cameras. These were placed in opposing parallel perspectives to enable individual identification of leopards, wild dogs, and elands. In order for the flash of one camera to not affect the other, they were not placed face to face but a few meters apart. The cameras had two different battery systems, ones with lithium 90-day life batteries were placed in the most secluded or hard to access stations, whereas the other, 40-day life battery, cameras were more accessible and thus enabled the changing of batteries and SD card throughout the study period. Out of 72 camera trap stations, 3 malfunctioned for the duration of the whole study, thus only 69 were operational (see Figure 7). For the purpose of the thesis, only data from the operational stations was utilised. The stations were on average at a 3km distance from each other, and a total area of more than 1500km^2 was covered. The study period was from the 12th of March 2021 to the 28th of June 2021, with a total of 11,082 camera trap days. More than 121,000 photographs were taken, of those 1,091 were identified as containing Roan. It is important to note that the placement of camera trap stations was not systematic for targeting Roan, as the goals of the project meant they were positioned in areas likely to have leopard activity. This meant they were placed in areas with habitat type favoured by leopards, as well as where tracks of both leopards and their prey species (including Roan) were identified. Additionally, water points and dried out wide riverbeds were favoured for the likeliness of capturing the majority of species of interest. Furthermore, it is vital to take into account that the plateau of species detection and identification was not reached, thus the project and consequently this thesis, would have benefitted from either more camera trap stations or a longer study period.

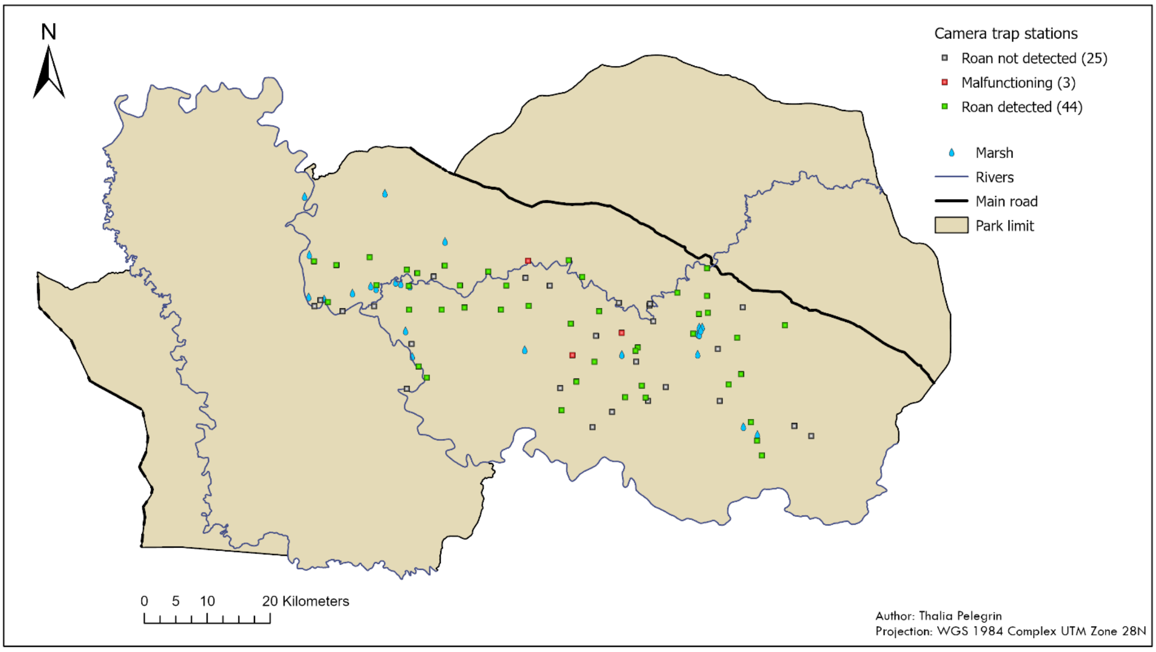


Figure 7: Map of NKNP with positions of camera trap stations and information about their functioning

4.3. Species data preparation

Upon receiving the 1,091 photos identified as containing Roan, a manual filtration was performed and photos containing either no animals or species that were not Roan were removed from the dataset leaving 1,085 photos. Once this was completed, ‘events’ were created with time, date, and number of individuals recorded. These events were defined as detection of Roan at a particular station and were considered separate if more than one hour had passed in between them, as applied by several camera trap studies such as Gómez et al. (2005), and Baker (2015). There was a total of 283 events identified across 44 camera trap stations, however, the nature of the code used for modelling considered the length of an event (or occasion) as one calendar day, thus events that occurred on the same day at the same station were agglomerated into one, reducing the total number of events to 260 when running the SDM. Additionally, a matrix of detection history was created using information about the functioning of camera traps, as well as the detection of Roan, to be used as an input file for modelling the species distribution. Circular statistics were performed in the ORIANA package by Kovach (2011) using time as the dependent variable to analyse the daily activity patterns of Roan. In order to do this, the mean vector and circular standard deviation were calculated and then Rayleigh's Uniformity Test and Rao's Spacing Test were performed to determine whether the data was distributed in a uniform manner regardless of its bilaterality. Finally a density plot was created in R using the "overlap" package, as well as a Rose diagram outputted from ORIANA.

4.4. Environmental variable preparation

In order to look at the species distribution modelling of Roan in NKNP, different variables were necessary to enable predictions. For the purpose of this thesis solely environmental/ecological variables were used due to limited data availability on anthropogenic activities, specifically because the camera trap station design was set in the core of the NKNP and did not embrace areas of livestock encroachment and other human-related activities. These environmental variables were chosen and divided into four categories: topographical, hydrological, vegetational, and climatic data.

4.4.1. Topographical data

Two topographical characteristics were chosen to be used as variables: Digital Elevation Model (DEM) and slope.

DEM

DEM is a representation of the Earth's surface or topography excluding features such as trees or buildings. It can be created using various techniques, such as land surveying or spatial analysis. The output is often a raster layer with a defined pixel size and values correspond to the geographic elevation present. This study used a DEM available from the National Aeronautics and Space Administration (NASA) from their 2000 Shuttle Radar Topography Mission (SRTM). The layer was downloaded from 'Application for Extracting and Exploring Analysis Ready Samples' (AppEEARS), a website that enables users to access environmental data of a defined desired spatial extent to reduce the amount of processing required (AppEEARS Team 2023). The specific DEM layer downloaded was 'SRTMGL1.v003', at a resolution of 1-arc second (approximately 30m cell size) and only included data within the limits of NKNP (NASA JPL 2013). The layer was then prepared by projecting it into the coordinate system used throughout the study (WGS_1984_Complex_UTM_Zone_28N), and values were extracted for each station. All data preparation for this layer and all subsequent layers was performed in ArcGIS Pro version 3.0.3 (ESRI 2022).

Slope

Slope is calculated from DEM as the rate of change of elevation by looking at the gradient in each cell. This was done using a spatial analyst tool called ‘slope’ and defined as change of elevation in degrees (values ranging from 0-90º). Therefore, the cell size was also approximately 30m. The values for each station were then extracted from the new layer. The decision to use slope in addition to DEM as a topographical variable was made after consideration of movement of species, where certain species are equipped to deal with steep habitats, whereas others actively avoid those areas. Studies on Roan have not discussed slope as a variable of distribution or habitat selectivity, thus investigation was beneficial.

4.4.2. Hydrological data

The study area contains two main water resource types: rivers and marshes. These are found in two completely different habitats, with different vegetation and other environmental conditions and are thus both important to consider separately, as animals may use them for different purposes. In order to gain an insight of the importance of hydrological variables on Roan distribution, distance to these variables was calculated.

Distance to river (DistRiv)

In order to do this, a shapefile of the permanent rivers was provided by the DPN at a 50m resolution, taking into account the study period was during the dry season. Using the ‘Euclidean distance’ spatial analyst tool, the distance to the nearest river was calculated creating a new layer and values were extracted per station.

Distance to marsh (DistMar)

Similarly, the shapefile of permanent marshes (50m resolution) was also obtained from the DPN, and the same process was performed as for the river shapefile in order to create a new layer with the distance to marshes.

4.4.3. Vegetational data

Two different vegetational indices were used as variables in the modelling: Normalized Difference Vegetation Index (NDVI) and above-ground woody biomass (AGB).

NDVI

NDVI is a vegetation index that calculates the ‘greenness’ of an area, which is typically correlated with amount of vegetation or biomass. Healthy vegetation is considered green (due to high levels of chlorophyll) and absorbs red light whilst reflecting infra-red light. Therefore, by measuring the difference between those two bands (in the wavelength spectrum of light) it provides a value which if high can be considered as dense vegetation. For the purpose of this study, NDVI dataset produced by the satellite-based sensor ‘Moderate Resolution Imaging Spectroradiometer’ (MODIS) was used (Didan 2021). The data was provided at 16-day intervals, which meant that several layers were downloaded to temporally cover the study period. Only this ‘dry season NDVI’ was applied, rather than using an annual NDVI, since the difference in vegetation is drastic between seasons and therefore cannot be representative within our study unless we also had species data for both the dry and wet season to compare. The layers had a 250m resolution and were downloaded from the AppEEARS website (AppEEARS Team 2023). Once projected into the correct coordinate system, the layers were merged to provide an average NDVI value per cell for the whole study period. Further statistics were performed to create a layer of the standard deviation of these values and extracted for each station (NDVI_SD).

AGB

Above-ground woody biomass is an important metric used in many studies when looking at carbon storage of large areas. However, on the African continent, it can also be used as a predictor of species distribution (particularly herbivores) due to the relationship with browsing and grazing material available. For the purpose of this study an AGB layer on the African continental scale was provided by Bouvet et al. (2018) at a 50m spatial resolution. They created their AGB layer using a combination of ground-based data and the 2010 Advanced Land Observing Satellite-Phased Array L-band Synthetic Aperture Radar (ALOS-PALSAR) data produced by the Japan Aerospace Exploration Agency (JAXA). The use of L-band frequency for AGB is quite useful in terms of classifying tree and canopy differences due to its high flexibility and low disturbance via rain and cloud cover (Aoki et al. 2021). In order to account for seasonality (which has significant changes on habitats in Africa), a Bayesian inversion was performed on the dry and wet seasons. The unit of measurement used in the layer was Megagrams per hectare (Mg.ha^{-1}), which represents the tree and shrub biomass. Once the layer was provided, clipped and projected, values were extracted per station.

4.4.4. Climatic data

Using climatic data can provide insight on which factors or variables are the most meaningful to the distribution of a species. The data is divided principally into two classifications: temperature-related and precipitation-related. For this study 19 bioclimatic variables were downloaded from the WorldClim database (version 2, Fick & Hijmans 2017). These variables are considered particularly useful for species distribution modelling and were created using the mean monthly climatic data collected in different weather stations and interpolated together between the years 1970-2000. The layers were downloaded at a 30-arc second resolution (approximately 1km cell size), which was the highest resolution available. The layers were prepared by clipping them to the shape of NKNP limits and then projecting them into the correct coordinate system. Then, with the visualisation of the layers, in addition to the knowledge of Roan species biology, the majority of bioclimatic variables were removed due to their limited biological significance and variability within the scope of this study leaving only five.

- Mean annual temperature (bio1)
- Temperature seasonality (bio4)
- Maximum temperature of the warmest month (bio5)
- Annual precipitation (bio12)
- Precipitation seasonality (bio15).

4.4.5. Correlation matrix

As an additional preparation for the modelling, a Pearson's correlation was run for all variables in order to assess which variables were highly correlated (see Figure 8). This was essential to determine for further model selection, evaluation and interpretation, as highly correlated variables placed in models together can lead to misinterpretation of their individual and overall significance on distribution of Roan. The correlation was also performed using p-values with a significance level of 0.05, which was then compiled with Pearson’s correlation coefficient to evaluate whether certain variables should be removed before running models (see Table 2). These analyses were performed using RStudio with R version 4.2.2 (RStudio Team 2022).

Upon evaluating the values of the correlation run, it became apparent that certain variables were strongly correlated and needed to be removed before modelling in order to minimise their influence on the model strength. DEM and the DistRiv were strongly positively correlated so the decision was made to remove DistRiv as a variable. The reasons for this are that DEM informs us not only on the difference change in elevation but also the changes in habitat types, due to the specific topography of NKNP which constitutes of plateaus of different habitats. Additionally, Roan, being a generalist species, seem to not be strictly water-dependent, hence removing the DistRiv whilst keeping DistMar enables us to still take into account distance to water. Bio5, which was strongly positively correlated with bio1, was removed as it was less informative on a yearly scope. Finally, bio12 and bio15 were removed due to their strong correlation both with each other and DEM. The decision to prioritize other categories of variables over the climatic ones were mainly based on the fact that the climatic variables and data available are much less variable, on the scale size of NKNP, and their resolution is significantly lower than other layers, which affects interpretation and representability.

Table 2: Pearson correlation matrix of environmental variables, where P-values are displayed on the right side of division, and correlation coefficient values on the left side. Elements in red represent very high correlation in terms of both correlation coefficient and significant P-values, whereas green ones represent elements with significant P-values but moderate correlation coefficient values.

	DEM	SLOPE	DistRiv	DistMar	NDVI	NDVI_SD	AGB	bio1	bio4	bio5	bio12	bio15
DEM		0.0363	0.0000	0.0546	0.0288	0.0033	0.0392	0.0012	0.0060	0.0175	0.0000	0.0000
SLOPE	0.25		0.0012	0.5526	0.0102	0.5286	0.1539	0.5147	0.0732	0.3932	0.0983	0.2066
DistRiv	0.84	0.38		0.4058	0.0009	0.0111	0.1174	0.1366	0.0000	0.9706	0.0000	0.0000
DistMar	0.23	-0.07	0.10		0.4723	0.4426	0.2107	0.0032	0.2273	0.0004	0.2199	0.0443
NDVI	0.26	0.31	0.39	-0.09		0.9372	0.0001	0.0452	0.0075	0.0139	0.0006	0.0008
NDVI_SD	0.35	-0.08	0.30	0.09	0.00		0.7813	0.0281	0.5913	0.1004	0.0232	0.0112
AGB	0.25	0.17	0.19	0.15	0.44	0.00		0.8339	0.2407	0.3274	0.0192	0.0263
bio1	0.38	-0.08	0.18	0.35	-0.24	0.26	0.00		0.2181	0.0000	0.0004	0.0000
bio4	-0.33	-0.22	-0.55	0.15	-0.32	-0.07	0.14	0.15		0.0000	0.0005	0.0005
bio5	0.29	-0.10	0.00	0.41	-0.29	0.20	0.12	0.89	0.53		0.0200	0.0078
bio12	0.79	0.20	0.71	0.15	0.40	0.27	0.28	0.42	-0.41	0.28		0.0000
bio15	-0.83	-0.15	-0.73	-0.24	-0.39	-0.30	-0.27	-0.47	0.41	-0.32	-0.97	

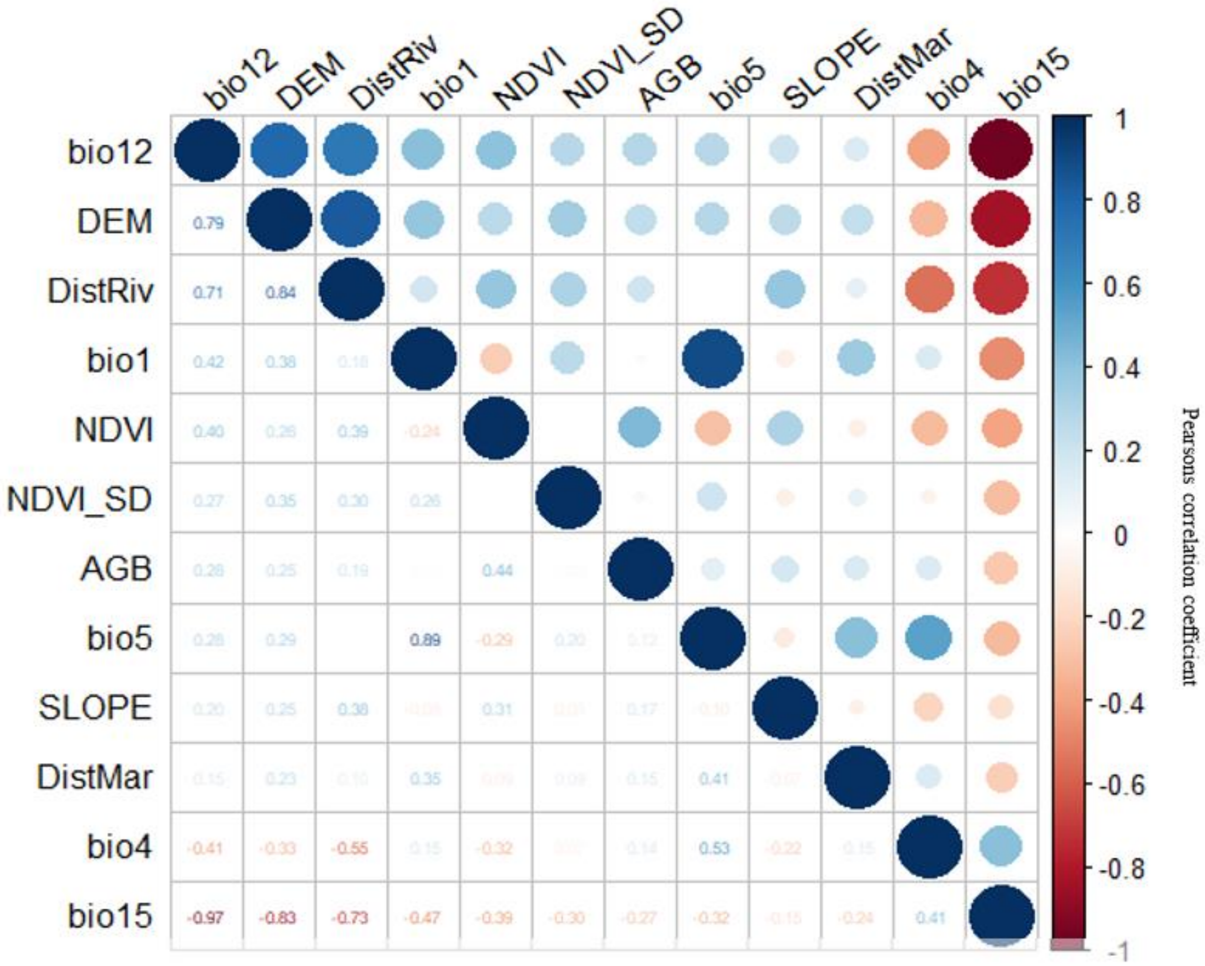


Figure 8: Pearson correlation coefficient matrix of environmental variables

4.5. Area of interest

Upon visualising the placement of the camera traps in NKNP it was unclear whether predictions over the whole of the park would be representative from the data collected. This was further supported by Rabeil et al. (2018) terrestrial and aerial surveys clearly displaying the presence of Roan outside of the areas surveyed by the stations included in this thesis (Figure 9). Therefore, a smaller area of interest (AOI) was created around the stations. This was done by drawing a polygon using the park border to the North and South, the main road to the East, and the Gambia River to the West as limits of the AOI (Figure 10).

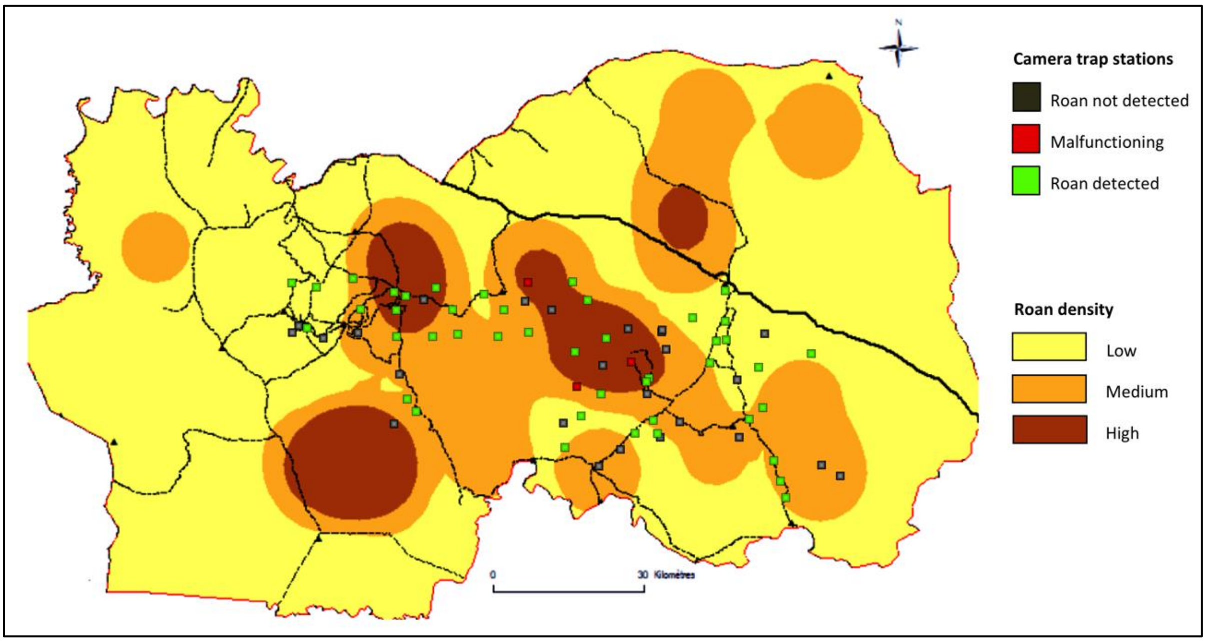


Figure 9: Map of aerial density estimates of Roan from Rabeil et al. (2018), adapted to include camera trap station positions used in this study

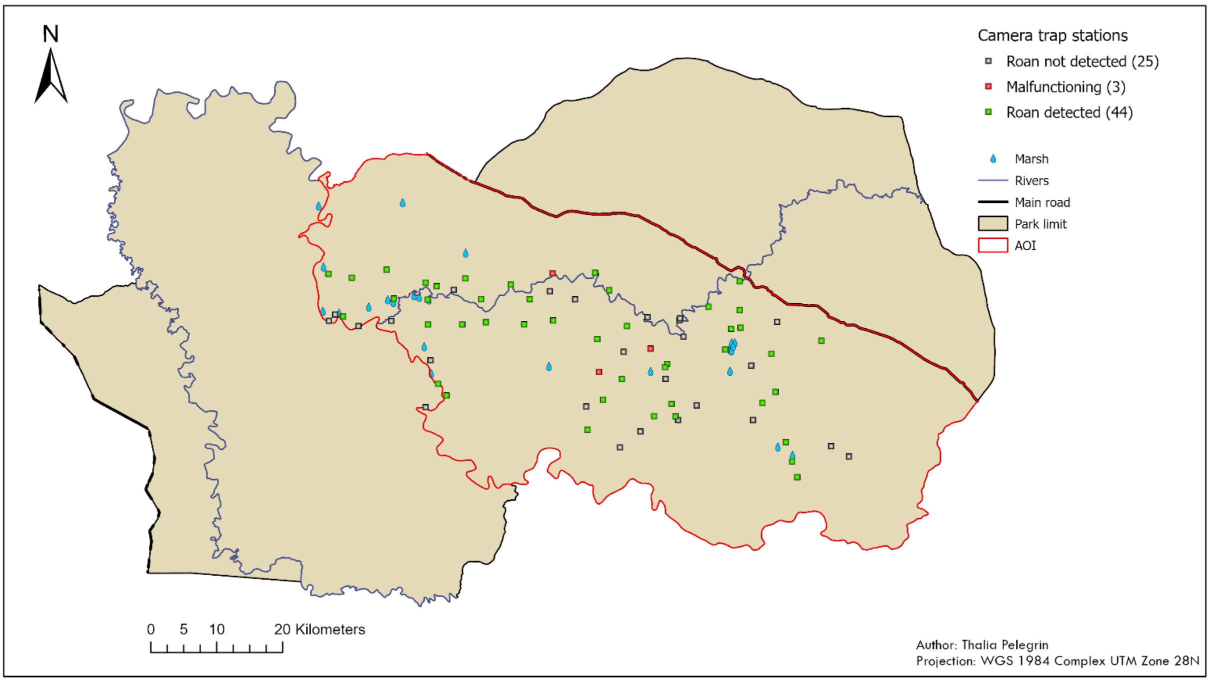


Figure 10: Area of interest (AOI)

4.6. Modelling

The species distribution modelling of Roan was performed in RStudio using R version 4.2.2 (RStudio Team 2022). The principal package to fit models and predict species distribution was ‘unmarked’ (Fiske & Chandler 2011). Below is a concise summary of the different steps taken to create the SDM. Additionally, the complete R code can be found in the Appendix 1 for further consultation.

After running the correlation matrix and removing the environmental variables that were strongly correlated, the next step was to run SDM. In order to do this, the detection matrix of Roan events was input into R and an occupancy frame created. The scaled covariates were then added to the frame so that models could be run. A first model was run (m1), which did not include any environmental variables to first evaluate the naïve occupancy. A back-transformation was then performed to allow us to understand the relative probability of occupancy, and comparing it to the final model to enable a better understanding of the relative influence of variables selected for it. It is important to clarify that models were run in two different ways: the first was on an exploratory basis, by individually selecting which variables to include, and the second was using the ‘dredge’ function, which computed all possible models with a combination of the different variables and classified them, in this case using the lowest Akaike Information Criterion (AIC) and delta values.

Once this was done, the next step was the process of model selection and its prediction across the area of both NKNP and the AOI created. In order to do this, rasters of the environmental variables were input into R and prepared, so they all had the same resolution (50m) and extent, before being stacked. Finally, after running the predictions, and their back-transformation, maps were created and several statistical tests were conducted in order to evaluate the performance of the SDM run. These tests measured overall fitness of the model by looking at the differences between the observed versus predicted values and determining whether they were statistically significant. The three tests used were the sum of squared errors (SSE), the chi-squared, and the Freeman-Tukey statistical tests. They all work in a similar fashion, comparing and investigating the discrepancies between the observed values and expected ones in relation to the prediction, although it is good to note that the Freeman-Tukey test in particular is valuable when using count data like Roan occurrence. They offer insight on the models effectiveness in successfully representing the patterns in the data, or in simpler words provide an overview of the general ‘goodness of fit’ of the model.

5. Results

5.1. Camera activity

Understanding the dispersal of Roan in terms of camera trapping activity is important to evaluate whether there are clear hotspots within our study area where Roan are more likely to be detected, and thus have a higher likelihood of occurring. Out of the 69 active camera stations, 44 identified Roan, thus a detection rate or naïve occupancy of 63% occurred. The basic visualisation of the number of events at each camera station can be seen on Figure 11 where the highest number of events for one camera station was 33. Additionally, for a better understanding of their population dynamics, a histogram was created presenting how many Roan individuals were detected per event, revealing predominantly a lot of solitary movement although a group of up to 12 individuals was detected (Figure 12).

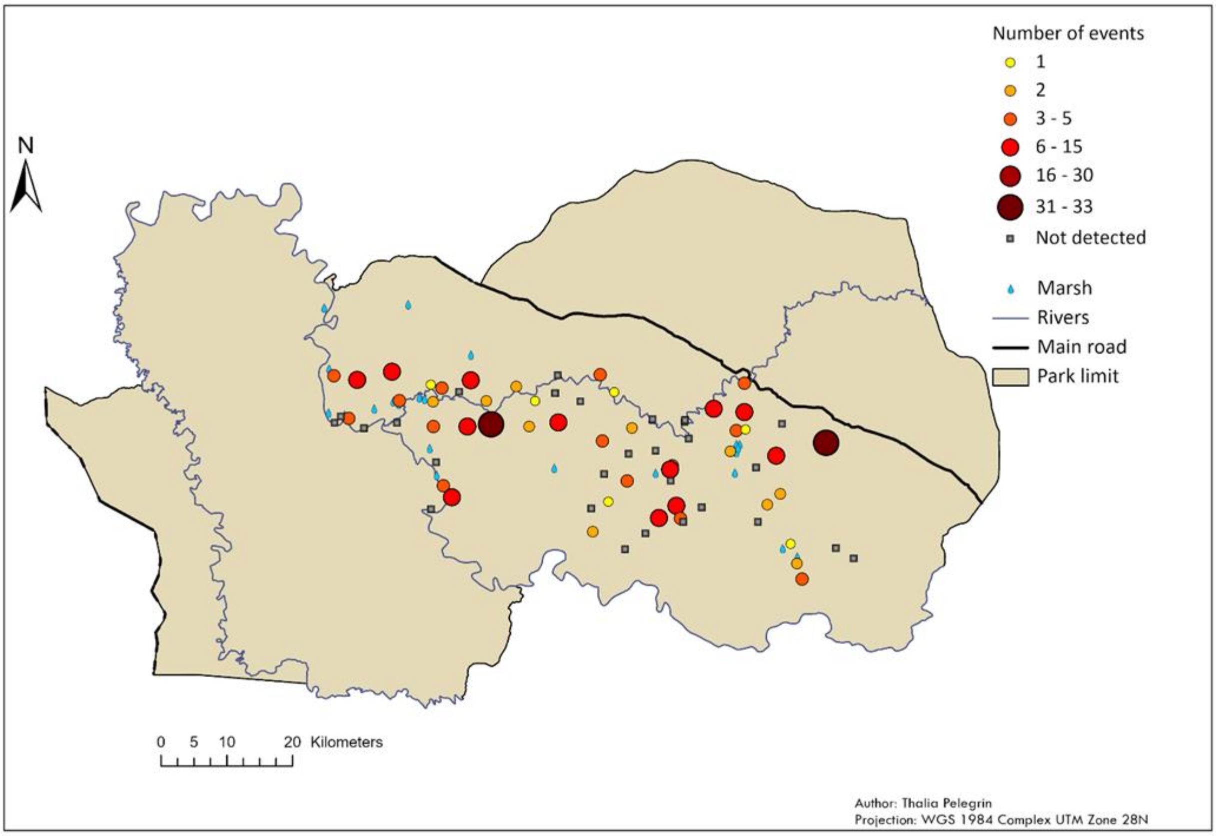


Figure 11: Number of detection events of Roan per station. Note that size of circles demarcates frequency of events at stations, not the surface area covered in reality

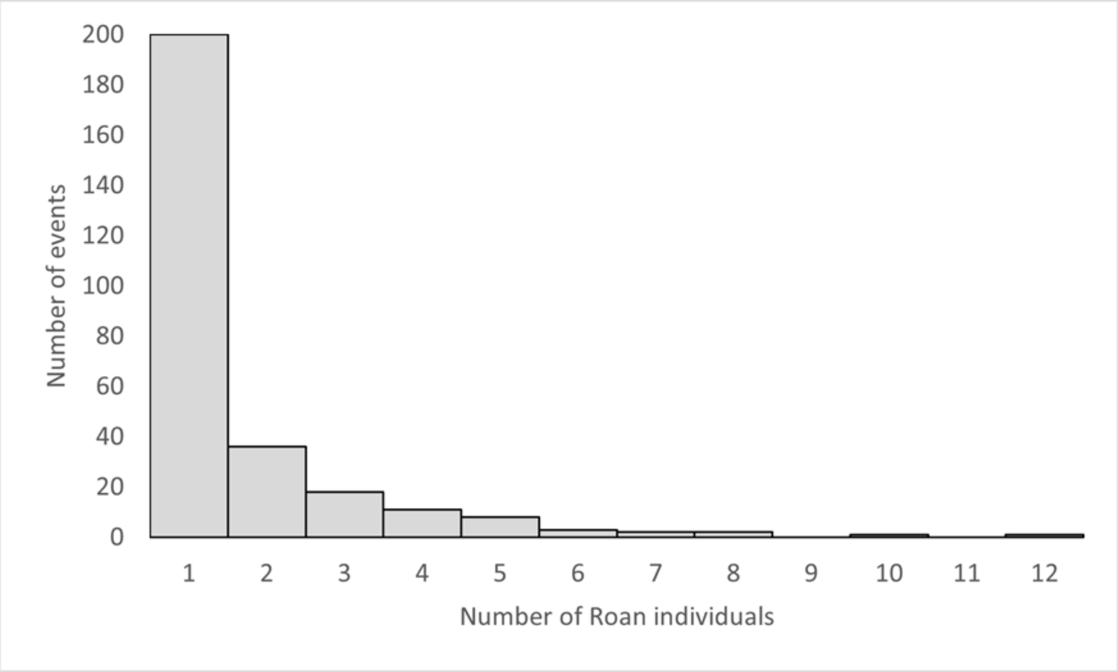


Figure 12: Histogram depicting number of roan individuals captured in detection events

Further investigation was conducted on the sex of the individuals found in the raw images of the 200 ‘solitary’ events (ones where only one Roan was detected). Of these, in 39 images (19.5%) the sex of the animal could not be determined. However, of the remaining images 63% (126) were males, 14.5% (29) were females, and 3% (6) were juveniles.

5.2. Species circadian activity

Based on the circular statistics performed, Roan activity in NKNP was diurnal with both Rayleigh’s Uniformity test and Rao’s Spacing test having a p-value of less than 0.05 (0.000 and 0.01, respectively). The rose diagram created clearly shows very little activity during the night, and a small activity peak after dawn (6am) and another longer one at midday until dusk around 6pm (Figure 13). Additionally, the density plot created in R indicated similar daily patterns of activity, predominantly higher density during the daylight hours, with the highest being right after midday (Figure 14). It was also revealed during the sorting of species data that the majority of events occurring post-sunset were solitary males.

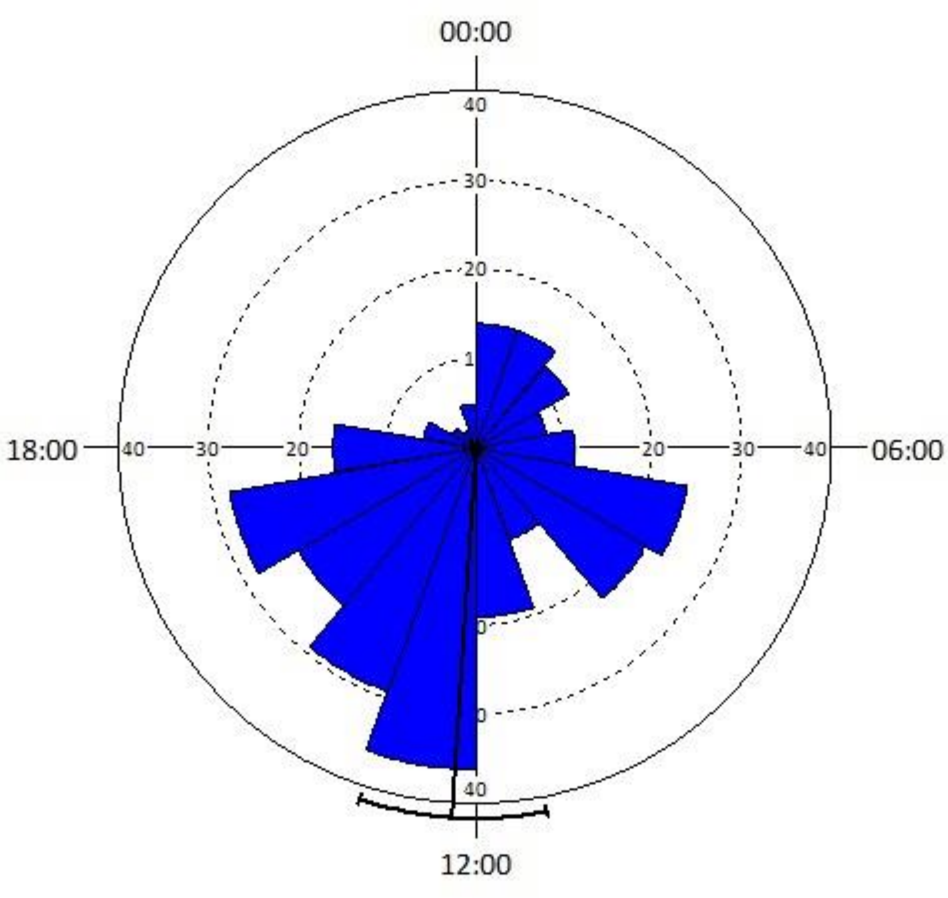


Figure 13: Rose diagram depicting daily activity pattern of Roan

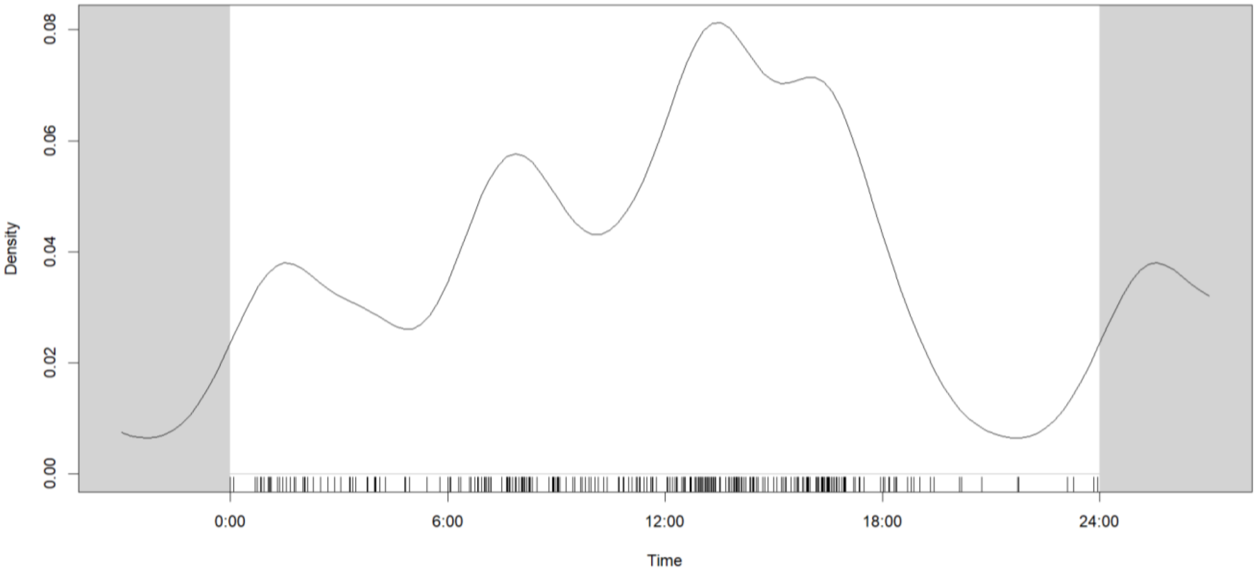


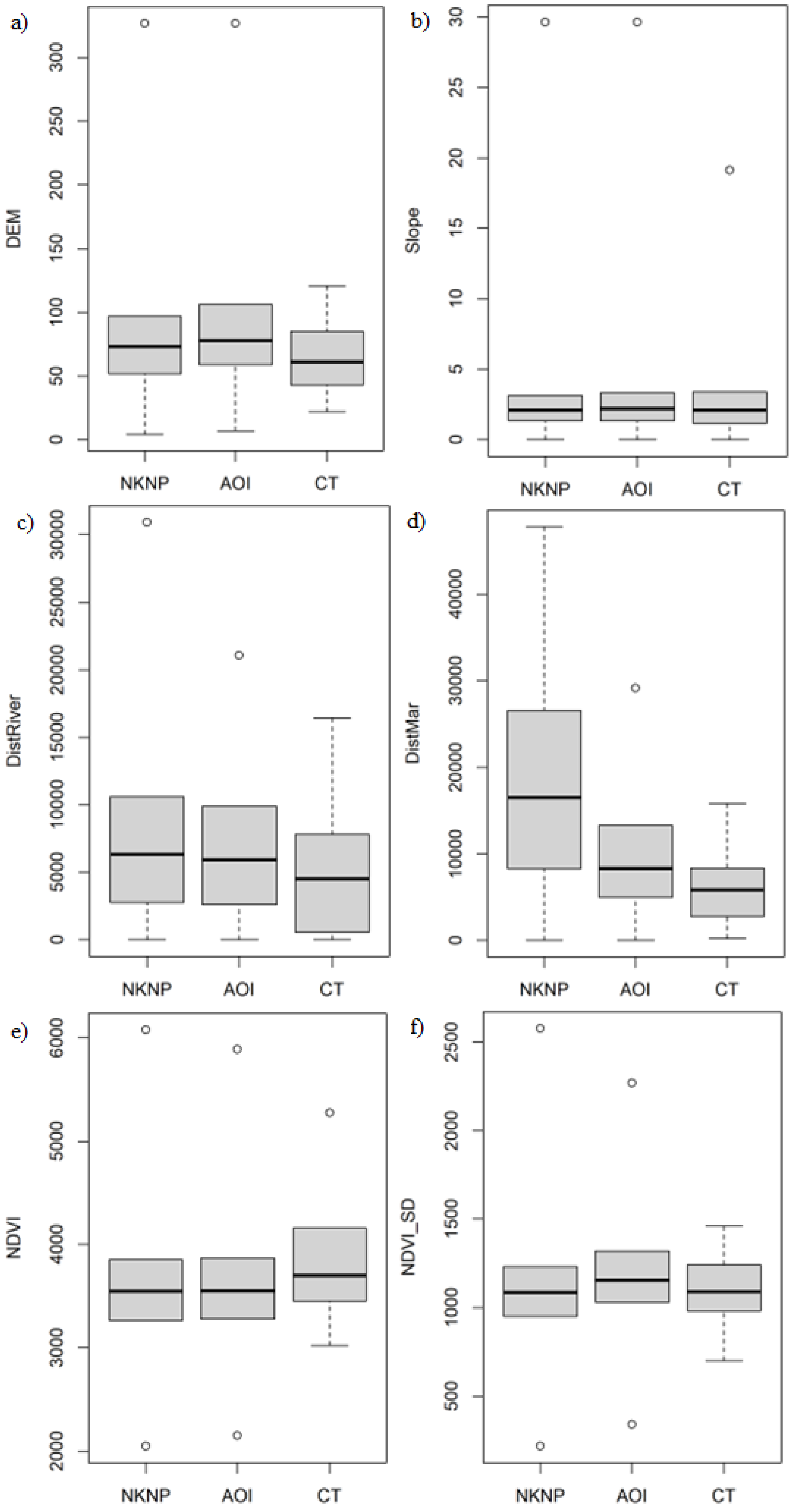
Figure 14: Density plot of Roan

5.3. Environmental variables

The descriptive statistics of all the environmental variables identified for the area of NKNP, the AOI, and the locations covered by the camera traps was summarized in Table 3. The decision to show the statistics of the variables at these different levels is to provide justification for predicting SDM both at an area of interest level and the national park level, and to help understand whether our camera trap data was representative. By looking at the mean value of each different area, it was clear that all the climatic variables had very narrow ranges within NKNP and thus the AOI and the smaller camera trap (CT) study area. DistRiv, DistMar and AGB however, had a clear difference in mean values between NKNP and the camera trap data collected. Additionally, boxplots were created in R for all environmental variables for visual aid in representativeness of data across the different levels (Figure 15). Moreover, rasters of the environmental variables were output for a visual representation and can be found in Appendix 2.

Table 3: Descriptive statistics of the environmental variables selected across different levels (NKNP, AOI, and camera trap).

	DEM	**Slope**	**DistRiv**	**DistMar**	**NDVI**	**NDVI_SD**	**AGB**	**Bio1**	**Bio4**	**Bio5**	**Bio12**	**Bio15**
NKNP												
Min	4	0	0	0	2047	218.06	1	27.09	233.58	37.70	804	125.03
1st Q	52	1.36	2750	8287	3267	951	12	27.60	245	38.60	890	127
Median	73	2.11	6329.49	16508.56	3548	1086.66	24	27.92	247.83	38.90	947	128.55
Mean	77.33	2.53	7369.48	17826.36	3577.04	1094.20	29.47	27.86	247.86	38.87	952.62	128.39
3rd Q	97	3.13	10602	26562	3851	1232	47	28.10	251	39.2	1010	130
Max	327	29.64	30912.78	47801.31	6078	2577.44	74	28.52	262.21	40	1133	131.42
AOI												
Min	7	0	0	0	2150	340.79	1	27.34	233.58	38	837	125.03
1st Q	59	1.36	2610	4988	3279	1031	10	27.90	244	38.80	917	127
Median	78	2.21	5912.91	8318.65	3552	1154.89	22	28.02	246.93	39	974	127.62
Mean	84.36	2.74	6660.45	9432.42	3584.03	1180.97	27.70	28.02	247.21	39.03	966.99	127.63
3rd Q	106	3.31	9872	13293	3865	1319	43	28.1	250	39.20	1015	129
Max	327	29.64	21069.23	29176.02	5887	2268.26	74	28.52	259.66	40	1082	130.14
Camera traps												
Min	22	0	0	200	3020	699.88	3	27.74	236.91	38.50	882	126.11
1st Q	43	1.19	565.69	2766.32	3449	981.62	23	27.99	245.06	38.90	920	127.05
Median	61	2.11	4531	5825.16	3701	1091.06	43	28.10	248.42	39.10	951	127.93
Mean	64.68	2.63	4860.43	5883.38	3851.81	1103.92	41.83	28.05	248.01	39.09	956.78	127.86
3rd Q	85	3.39	7823.04	8386.30	4160	1240.90	60	28.14	251.01	39.30	992	128.51
Max	121	19.12	16422.90	15809.60	5276	1462.96	73	28.25	259.21	39.50	1046	129.77


a)
DEM
0
50
100
150
200
250
300
NKNP
AOI
CT
b)
Slope
0
5
10
15
20
25
30
NKNP
AOI
CT
c)
DistRiver
0
5000
10000
15000
20000
25000
30000
NKNP
AOI
CT
d)
DistMar
0
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30000
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NKNP
AOI
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NDVI
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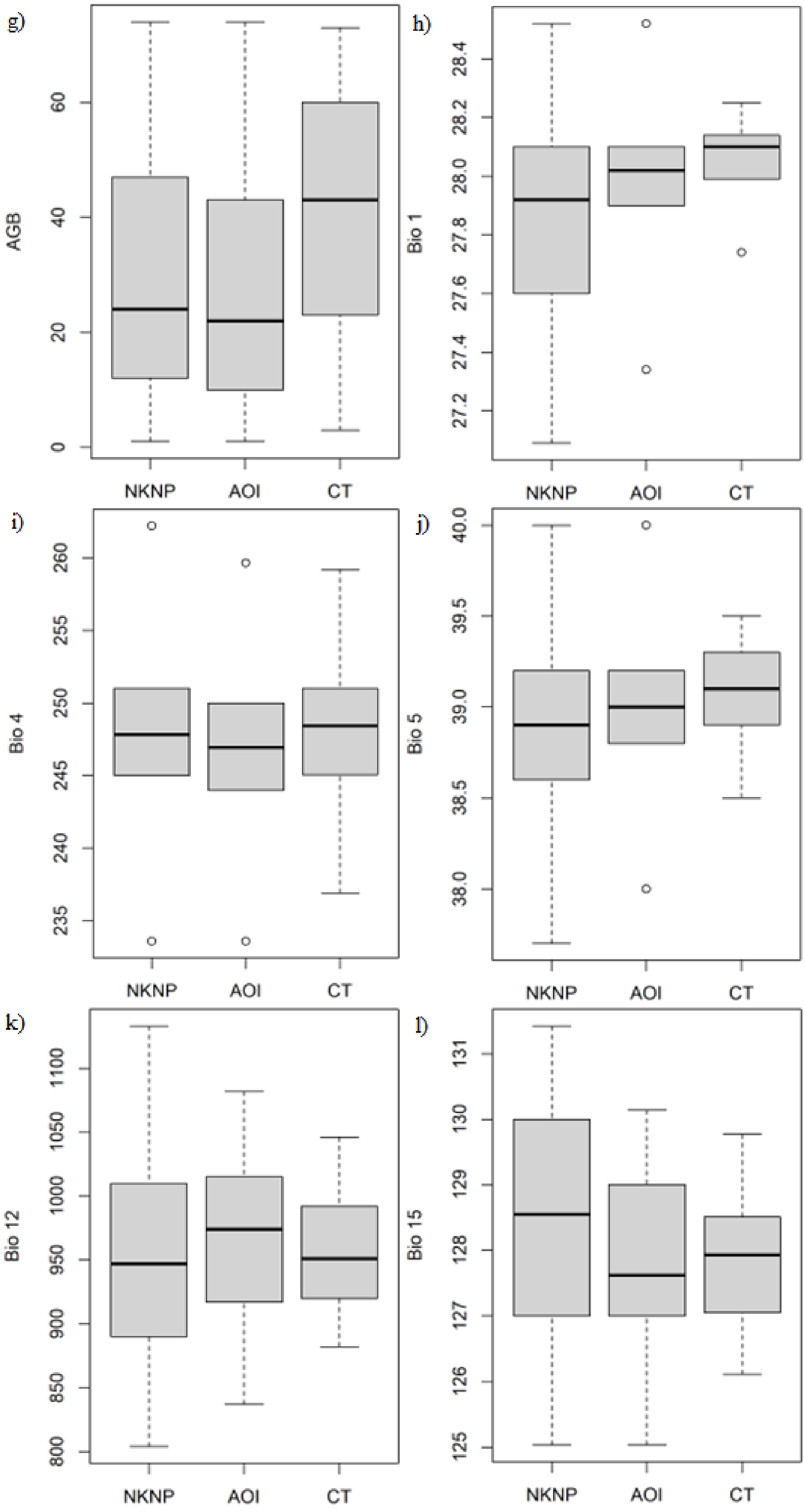
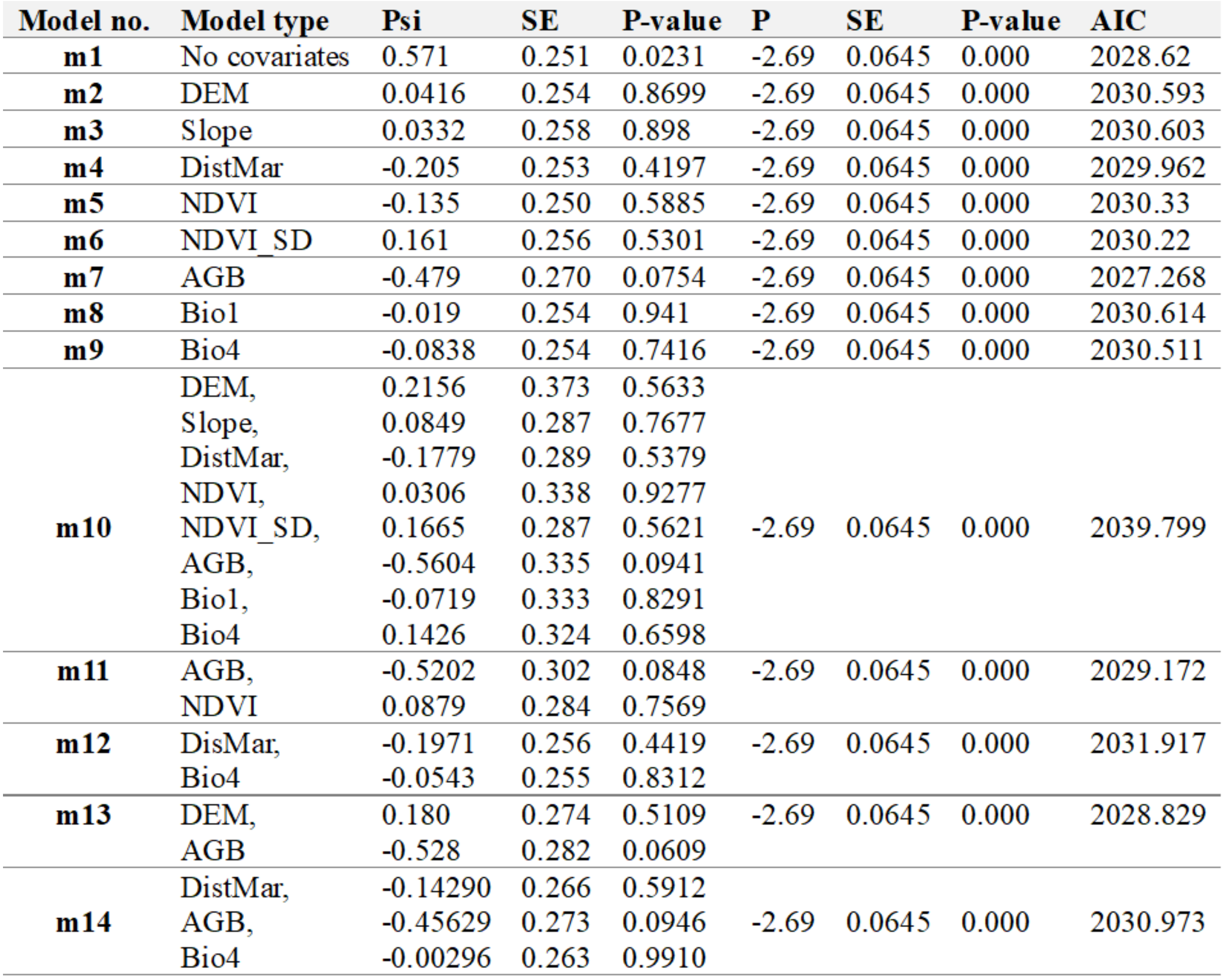


Figure 15: Boxplots of environmental variables (a-l) at different levels (NKNP, AOI, CT)

5.4. Model selection

The models were initially run in an exploratory manner as can be seen on Table 4 by first looking at probability of occupancy (Psi) of Roan without any environmental variables (m1), and then using only a single variable at a time (m2-m9). A model was then run using all the environmental variables selected (m10) in addition to several others performed using a mix of two or three variables (m11-m14). The p-values of all models with environmental variables were above 0.05, however, the model run with AGB only (m7) had the smallest p-value at 0.07. In order to compare these models to each other, a cumulative performance was created and summarized in Table 5, indicating indeed that m7 was the most explanatory due to the lowest AIC value (2027.27) and thus the delta value equal to 0.00. All models were run with the probability of detection (P) remaining a constant variable.

Table 4: Exploratory model results where Psi is probability of occupancy and P is probability of detection



Model no.	Model type	Psi	SE	P-value	P	SE	P-value	AIC
m1	No covariates	0.571	0.251	0.0231	-2.69	0.0645	0.000	2028.62
m2	DEM	0.0416	0.254	0.8699	-2.69	0.0645	0.000	2030.593
m3	Slope	0.0332	0.258	0.898	-2.69	0.0645	0.000	2030.603
m4	DistMar	-0.205	0.253	0.4197	-2.69	0.0645	0.000	2029.962
m5	NDVI	-0.135	0.250	0.5885	-2.69	0.0645	0.000	2030.33
m6	NDVI_SD	0.161	0.256	0.5301	-2.69	0.0645	0.000	2030.22
m7	AGB	-0.479	0.270	0.0754	-2.69	0.0645	0.000	2027.268
m8	Bio1	-0.019	0.254	0.941	-2.69	0.0645	0.000	2030.614
m9	Bio4	-0.0838	0.254	0.7416	-2.69	0.0645	0.000	2030.511
m10	DEM,	0.2156	0.373	0.5633	-2.69	0.0645	0.000	2039.799
	Slope,	0.0849	0.287	0.7677				
	DistMar,	-0.1779	0.289	0.5379				
	NDVI,	0.0306	0.338	0.9277				
	NDVI_SD,	0.1665	0.287	0.5621				
	AGB,	-0.5604	0.335	0.0941				
	Bio1,	-0.0719	0.333	0.8291				
	Bio4	0.1426	0.324	0.6598				
m11	AGB,	-0.5202	0.302	0.0848	-2.69	0.0645	0.000	2029.172
	NDVI	0.0879	0.284	0.7569				
m12	DisMar,	-0.1971	0.256	0.4419	-2.69	0.0645	0.000	2031.917
	Bio4	-0.0543	0.255	0.8312				
m13	DEM,	0.180	0.274	0.5109	-2.69	0.0645	0.000	2028.829
	AGB	-0.528	0.282	0.0609				
m14	DistMar,	-0.14290	0.266	0.5912	-2.69	0.0645	0.000	2030.973
	AGB,	-0.45629	0.273	0.0946				
	Bio4	-0.00296	0.263	0.9910				

Table 5: Cumulative performance of exploratory models run, ranked by delta value

Model no.	Model type	AIC	Delta value	AIC weight	Cumulative weight
m7	AGB	2027.27	0.00	0.24523	0.25
m1	No covariates	2028.62	1.35	0.12473	0.37
m13	DEM, AGB	2028.83	1.56	0.11236	0.48
m11	AGB, NDVI	2029.17	1.90	0.09467	0.58
m4	DistMar	2029.96	2.69	0.06375	0.64
m6	NDVI_SD	2030.22	2.95	0.05604	0.70
m5	NDVI	2030.33	3.06	0.05304	0.75
m9	Bio4	2030.51	3.24	0.04847	0.80
m2	DEM	2030.59	3.33	0.04650	0.84
m3	Slope	2030.60	3.34	0.04627	0.89
m8	Bio1	2030.61	3.35	0.04602	0.94
m14	DistMar, AGB, Bio4	2030.97	3.71	0.03845	0.98
m12	DistMar, Bio4	2031.92	4.65	0.02399	1.00
m10	DEM, Slope, DistMar, NDVI, NDVI_SD, AGB, Bio1, Bio4	2039.80	12.53	0.00047	1.00

Before final model selection for predictions was done, a final model comparison was run using the ‘dredge’ function in R, enabling us to see all possible model combinations. A summary of the most explanatory models was selected based on delta values of less than two (Table 6). Once again, at the top of the list was the model using only AGB. Although the other models using environmental variables have a delta value of less than two and thus can still be explanatory, they all contain AGB as one of their variables. Therefore, for further predictions on both the NKNP and the AOI, the only model used was the one with solely AGB.

Table 6: Summary of dredge for top models with delta values less than two

Dredge model no.	P (Int)	psi (Int)	psi (AGBx)	psi (bio1x)	psi (bio4x)	psi (DEMx)	psi (DistMarx)	psi (NDVI_SDx)	psi (NDVIx)	psi (SLOPEx)	AIC	delta	weight
2	-2.68955	0.604352	-0.47913	NA	NA	NA	NA	NA	NA	NA	2027.268	0	0.058996
1	-2.68908	0.571235	NA	NA	NA	NA	NA	NA	NA	NA	2028.62	1.352074	0.030007
34	-2.68913	0.606778	-0.48474	NA	NA	NA	NA	0.179414	NA	NA	2028.788	1.519969	0.027591
10	-2.68911	0.608198	-0.52825	NA	NA	0.180364	NA	NA	NA	NA	2028.829	1.560918	0.027032
18	-2.68912	0.605256	-0.4566	NA	NA	NA	-0.14332	NA	NA	NA	2028.974	1.705606	0.025145
130	-2.68911	0.604396	-0.5	NA	NA	NA	NA	NA	NA	0.116079	2029.065	1.79684	0.024024
66	-2.68908	0.604432	-0.52018	NA	NA	NA	NA	NA	0.087902	NA	2029.172	1.90363	0.022775
6	-2.68907	0.603334	-0.47606	NA	-0.02199	NA	NA	NA	NA	NA	2029.261	1.992901	0.021781
4	-2.68912	0.603129	-0.47886	-0.00887	NA	NA	NA	NA	NA	NA	2029.267	1.998811	0.021716

5.5. Prediction and evaluation

After running the prediction of Roan distribution using the model with AGB as the environmental variable, maps were created indicating probability of occupancy both in NKNP and the AOI (see Figure 16 and Figure 17, respectively). These maps are gradually coloured with pixel values ranging from 0-1 where 1, which is in green, is the highest probability of occurrence. Upon visual comparison between the map created for NKNP and the AOI, the differences were found to be minimal, however, an AOI always remains useful practice before extrapolating to a greater area. It is clear from the predictions that the majority of the park has a moderately high Roan occupancy probability.

The results of the three statistical tests run to evaluate the model can be seen in Figure 18, and they enable us to assess whether our model can accurately portray the relationship between Roan occurrence and AGB in NKNP. The plots representing theses three tests can be interpreted using the dashed lines as the observed value and the histogram as the expected values. When observing this, it is apparent that the model does not have a perfect fit, however, it can still be determined as adequately explanatory when related to the selection procedure and delta and AIC values indicated. Moreover, although this was the best fit from the list of models created, it is important to acknowledge that there may be other contributing factors not encompassed in this study that may have a stronger effect on Roan distribution. This possibility will be explored in more detail in the discussion.

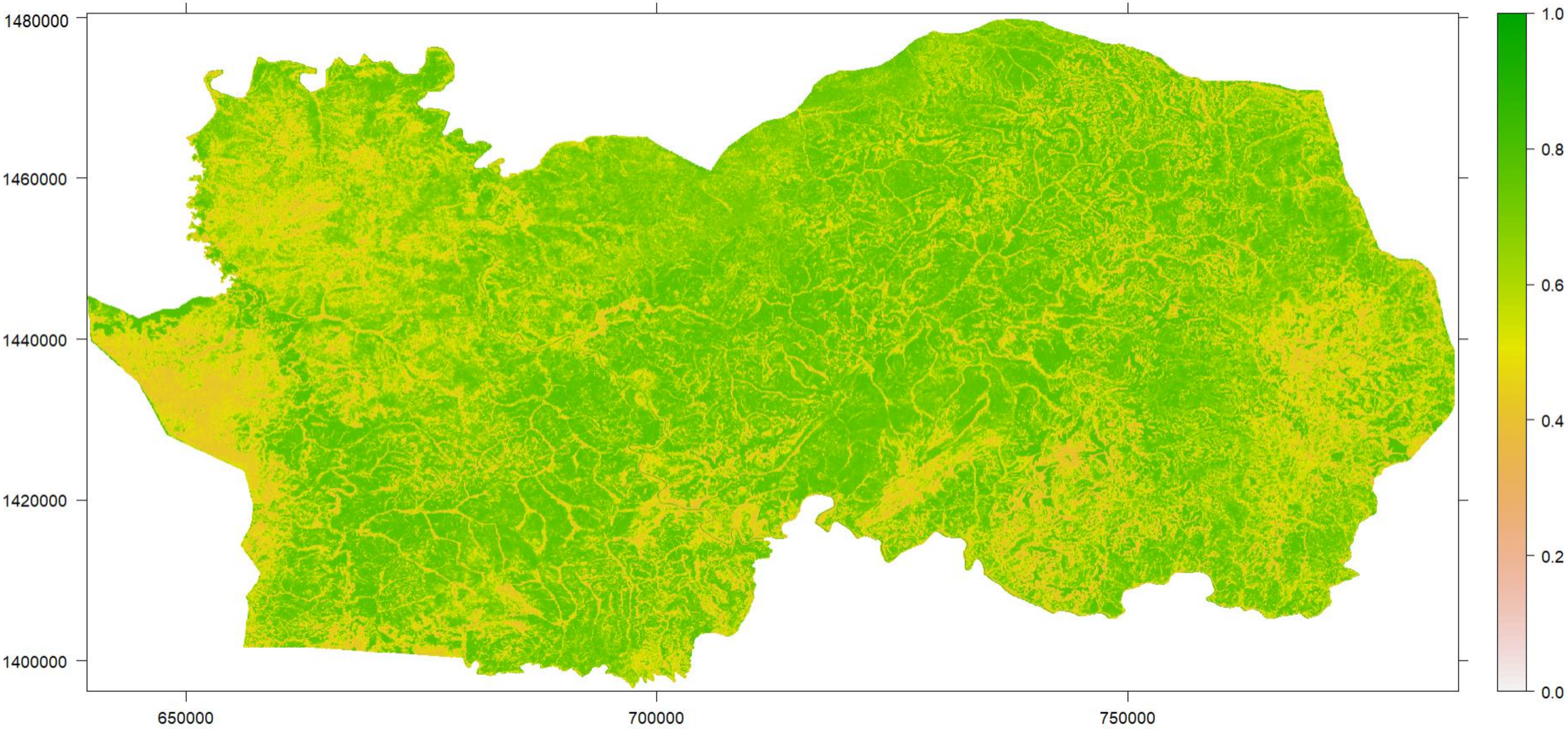


Figure 16: Prediction map of the probability of Roan occurrence/presence in NKNP

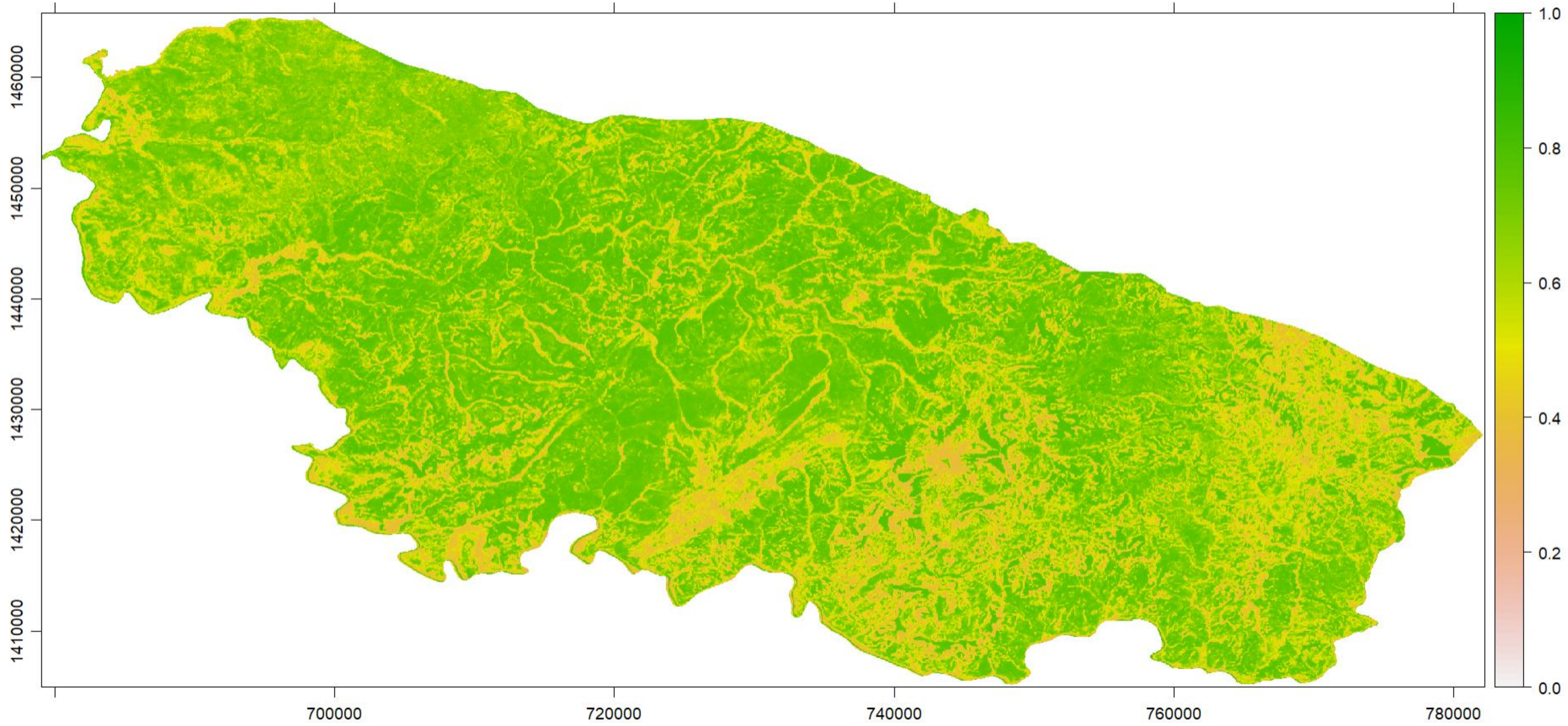


Figure 17: Prediction map of the probability of Roan occurrence/presence with the AOI inside NKNP

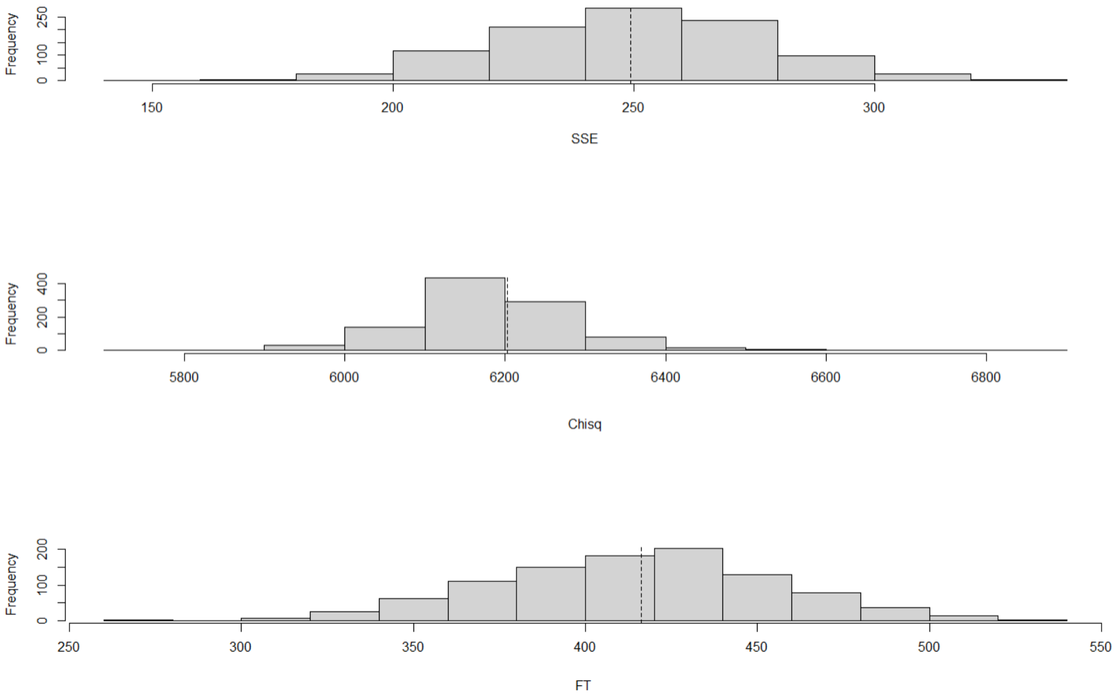


Figure 18: Statistical evaluation of prediction run on Roan distribution using SSE, Chi-squared and Freeman-Tukey tests. Histogram is composed of the expected values and the dashed lines represent the observed values output by the model

6. Discussion

A relatively high number of events were observed throughout the period of study, and they seemed to be distributed more or less uniformly across the study area, with the exception of two camera stations that each had more than 30 events (Figure 11). However, despite the detection rate being 63%, as mentioned previously in the methods, the plateau of species detection and identification was not reached during the study period (Drouilly et al. 2021). This consequently affects our SDMs which rely on our sampling to create presence-absence data, and an imperfect detection, whether it be through incomplete sampling or otherwise, can impact the resulting SDMs (Lahoz-Monfort et al. 2014; Martinez-Minaya et al. 2018). Nevertheless, this does not signify that the SDM created should be discarded, simply it reinforces the careful consideration that must be taken when evaluating it, and its importance in describing Roan distribution. Additionally, when looking at previous studies done on the distribution of Roan in NKNP, such as the aerial surveys described by Rabeil et al. (2018), it is clear that our study area limited by camera trap placement is not completely adequate as it does not encompass other areas (notably Southwest of our AOI, Figure 9) where Roan have been detected. Despite this, the species detection data remains valuable both to the SDM and to the development of our understanding on Roan.

The analysis of species activity is multifaceted, both looking at social behaviour in terms of social structure, and patterns of daily activity or circadian rhythm. From all the events compiled, up to 200 of them, or in other words more than 70%, detected only one Roan individual throughout the event (Figure 12). Although it seems like it, this statistic should not lead to the interpretation that Roan are predominantly solitary for two reasons. The first being that other events detected up to 12 individuals travelling together, displaying at the least temporary aggregations. Additionally from further investigation of images of solitary encounters, an assumption can be made that the images containing juveniles were not ‘solitary’ events, as it is highly unlikely for juveniles to be alone and far more plausible that other individuals were simply not captured during this event. Furthermore, and most importantly, the high occurrence of solitary males (63%) is consistent with literature stating the social dynamics of Roan can be divided into semi-gregarious nursing herds, and bachelor males often found alone or forming a herd (Chardonnet & Crosmary 2013). Moreover, the high detection of these males may be in part due to their drive to find resources including females to mate with, thus having increased daily movement patterns in comparison with the nursing herds, making them likelier to be caught by camera traps. However, it should be noted that definite conclusions on these daily movement patterns cannot be made, as Roan have not been individually recognised.

Aside from social structure, the data collected from the camera traps also allowed for statistical analysis of daily activity patterns. The results of this study align with aforementioned research, declaring Roan as predominantly diurnal (Castello 2016), since the majority of their activity is between the hours of 6am and 6pm (Figure 13). This is statistically significant, as both tests of uniformity performed resulted in p-values of less than 0.05, describing the data as not uniform across a 24-hour period. However, Castello (2016) also described two peaks throughout the day and very low activity just after noon, which are not as prevalent in this study, and contrastingly, the highest level of activity can be seen right after midday (Figure 14). A possible explanation for this may be linked to their water dependency as observed in a recent study by Kasiringua et al. (2017), which describes Roan as diurnal drinkers often found at waterholes during the daylight hours. A reason for this may be to avoid the potential for higher predation rates by nocturnal predators such as leopards, which are prevalent in NKNP, thus driving them to drink and move towards waterpoints throughout the day.

Individual variability of the environmental variables across the three levels of study (NKNP, AOI, and CTs) was noted to be reasonably similar in terms of range, which might indicate the representativeness of our small study area to be extrapolated over the whole region of the park. However, there were some exceptions that may be important to consider, particularly with the hydrological data. Both the range of the DistRiv and DistMar varied considerably between the NKNP and CT levels, halving and scaling down to a third of the distances recorded, respectively (Table 3), thus potentially leading to incongruencies in model interpretation if used. Additionally, the data collected to determine the distance of camera stations to marshes was found to be incomplete, and thus may be a false representation of the reality in NKNP. Therefore, although models were still run with it as a variable, since distance to water is closely related to water dependence in species, it was highly unlikely to be chosen within a final prediction model. Moreover, the lack of variability in range across levels of the climatic data variables (seen in Figure 15 h-l), affected the decision-making process of model selection. On one hand, using climatic data can inform us on the current and future state of a species distribution in changing climate, which has become extremely beneficial in conservation and policy-making decisions when used with precaution (Hallfors et al. 2016). On the other hand, using low resolution data, such as our 1km climate data, has been found to affect the performance of SDMs, and thus our interpretations of their result (Reside et al. 2011). Furthermore, the fact that the study period only encompasses the dry season and not the wet season, where climate data may be drastically different, reinforces the idea that NKNP is fairly homogenous in terms of climate which is not necessarily accurate. Therefore, in addition to DistMar and DistRiv, models that favoured climate data may have been placed under higher scrutiny. Additionally, this not only enforces the caution that must be taken when selecting a model, but also provides a powerful argument to have future studies use and compare SDMs throughout different seasons, in order to minimize misinterpretations or generalisations made.

The model selection process was done in a triumvirate manner in order to exhaust as many possibilities as possible before choosing the model to run the prediction (Tables 4,5,6). Note that only probability of occupancy was influenced, and detection was made to remain constant since there was no seasonal data, thus it stayed the same throughout space and time. Models were evaluated using their AIC values, which is a statistical measure of the balance between the goodness of fit of the model and its parsimony (how simple it is). The delta values were also used, which is a comparative weighting of AIC values to the best model. Both of these are critical when evaluating models and should be the lowest possible as an indication of robustness (Elith & Leathwick 2009). In all three trials of model running, the output with the lowest delta value of 0 and the lowest AIC value of 2027.268 was the one using AGB, ascertaining it as the most explanatory model for the probability of occurrence of Roan. Despite model evaluations using delta and AIC values being extremely crucial in model selection, it is equally important to relate this back to species biology and consider what is the best fit for understanding distribution (Guillera-Arroita et al. 2015). In this case, the importance of AGB to Roan is complex and can be linked to several factors, such as dietary requirements as well as habitat requirements for their young, in addition to a multitude of other influences which have not been explored such as predation risk, seasonality, or livestock encroachment. Nevertheless, it is still informative, and thus its extrapolation across both the AOI and NKNP provides us with useful information on the distribution of Roan.

The model prediction ran with AGB can be described as robust when looking at its goodness of fit in Figure 18, as the observed values for all three statistical tests performed sit within the bulk of the expected values. The map outputs portray a wide area of both the AOI and NKNP as having a high probability of Roan presence since the majority of the area is green (probability of occupancy=1) and only certain small individuals or patchy areas are yellow determining approximately 0.4 probability of occupancy (see Figure 16 and 17). The lack of visible pattern suggests that the general environment found in NKNP fulfils the basic requirements of Roan to survive and thrive. Above-ground woody biomass is used by Roan for different purposes, but particularly more for feeding during the dry season, so much so that they have been described to browse more than their grazing relatives during dry seasons (Hensman et al. 2012). This is understandable as they are considered dietarily fluid herbivores, and they have been found to have a digestive tract that is more adapted to digesting browse material than other grazers (Heitkonig 1993). Another possible reason for AGB to impact Roan distribution is its use for shade during the warmest period of the day, woody cover may provide relief from direct sunlight and enable less energy spent on thermoregulation (Veldhuis et al. 2019).

Although this prediction model permits us to better understand the potential distribution of Roan in NKNP, it does so through simplicity, and thus further studies may be more informative if additional variables are incorporated. However, an important consideration to take into account is the weakness of data availability from areas close to the borders of the park, since certain constraints, such as livestock encroachment, cannot be assessed. A previous study on habitat suitability of Roan in Kenya showed that anthropogenic factors did have an effect in predicting distribution of Roan, with the level of impact varying dependent on the season (Kimanzi et al. 2013). Furthermore, the climatic data, as previously discussed, may not be representative across seasons, and at its current resolution, further restricts the ability to identify them as contributing drivers of distribution. Therefore, it may be beneficial for future studies to focus on a larger area (potentially continental), if the goal is to assess the effect of climate on Roan distribution. Nevertheless, despite the limitations from the data, it is crucial to keep in mind that Roan are generalist species, described as having high adaptability, and thus have the potential to occur in a broad range of conditions due to their relatively ecologically homogenous functional niche. This can be identified within the scope of our study since the expected probability of occurrence (or naïve occupancy) of roan across all sites prior to implementing environmental variables into the model was 63.9% (0.639; SE 0.0580), and in the case when including AGB at its mean value, the probability of occupancy at all sites was 64.7% (0.647; SE 0.0595), which is not significantly different.

7. Conclusions

The use of camera trap data for presence-absence in SDMs has become a common way to conduct research to understand the distribution of different species and inform policy-making and conservation measures. This study aimed to use SDM to gain a better understanding of the distribution of the Roan antelope in NKNP using camera data and environmental variables from various sources. The models created led to the interpretation of Roan being highly likely to occur widely across the park, and that during the study period, which occurred within the dry season, above-ground woody biomass was the strongest predictor of distribution. However, the lack of base data both in terms of area in the rest of the park (specifically borders), as well as data availability, means that an exhaustive list of predictors has not been used and therefore, conclusions on the distribution of Roan must be handled with caution. Additionally, aside from environmental variables, anthropogenic factors tend to also have an effect on distribution, notably due to livestock and human encroachment. Therefore, future studies could incorporate anthropogenic variables in addition to other resources of impediments which could be critical to Roan distribution such as predation (distribution of predators). Moreover, due to the limitations of climate data available in its low resolution, it may be beneficial to include a comparison of distribution between different habitats in the present and future climate, across seasons, or across a wider range of distribution (such as on a continental scale). This would not only enable better understanding of how climate may affect Roan, but also may provide further insights into why there are differences in population trends between West and Southern Africa.

Nevertheless, although this thesis does not provide definitive conclusion on the distribution of Roan, it creates a basis of knowledge, which can be useful for future studies in understanding limitations of SDM, and in providing insight into the possible predictors in NKNP. Within the scope of this study and with the knowledge and understanding of the species being a generalist antelope, an assumption can be made that the area of NKNP seems to fulfil the basic habitat requirements of the species, thus resulting in high probability of occurrence or presence across the park.

8. References

Allsop R. 1979. Roan antelope population in the Lambwe valley, Kenya. Journal of Applied Ecology **16**: 109-115.

Alpers DL, van Vuuren BJ, Arctander P, Robinson TJ. 2004. Population genetics of roan antelope (*Hippotragus equinus*) with suggestions for conservation. Molecular Ecology **13**: 1771-1784.

Alpert P. 2005. Sharing the secrets of life without water. Integrative and Comparative Biology **45**: 683-684.

Anderson TM, White S, Davis B, Erhardt R, Palmer M, Swanson A, Kosmala M, Packer C. 2016. The spatial distribution of African savannah herbivores: species associations and habitat occupancy in a landscape context. Philosophical Transactions of the Royal Society B **371**: 1-14.

Ansell WFH. 1971. Order Artiodactyla. Pages 1-84 in Meester J, Setzer HW, editors. The mammals of Africa: an identification manual. Smithsonian Institution Press, Washington DC.

Aoki Y, Furuya M, De Zan F, Doin MP, Eineder M, Ohki M, Wright TJ. 2021. L-band Synthetic Aperture Radar: current and future applications to Earth sciences. Earth, Planets and Space **56**: 1-4.

AppEEARS Team. 2023. Application for Extracting and Exploring Analysis Ready Samples (AppEEARS). Ver. 3.26. Available from https://appeears.earthdatacloud.nasa.gov (accessed March 2023).

Archibald S, Bond WJ, Stock WD, Fairbanks DHK. 2005. Shaping the landscape: fire-grazer interactions in an African savanna. Ecological applications **15**: 96-109.

Aremu OT. 2004. Density, distribution and feeding strategies of roan antelope (*Hippotragus equinus*) in Borgu sector of Kainji lake national park, Nigeria. Ghana Journal of Science **44**: 39-45.

Austin MP. 1980. Searching for a model for use in vegetation analysis. Vegetation **42**: 11-21.

Austin MP. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecological Modelling **157**: 101-118.

Azzou SAK, Singer L, Aebischer T, Caduff M, Wolf B, Wegmann D. 2021. A sparse observation model to quantify species distributions and their overlap in space and time. Ecography **44**: 928-940.

Bailey DW, Gross JE, Laca EA, Rittenhouse LR, Coughenour MB, Swift DM, Sims PL. 1996. Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management **49**: 386-400.

Baisero D, Visconti P, Pacifici M, Cimatti M, Rondinini C. 2020. Projected global loss of mammal habitat due to land-use and climate change. One Earth **2**: 578-585.

Baker GM. 2015. Quantifying wildlife use of cave entrances using remote camera traps. Journal of Cave and Karst Studies **77**: 200-210.

Batavia C, Nelson MP. 2017. For goodness sake! What is intrinsic value and why should we care? Biological Conservation **209**: 366-376.

Beale CM, et al. 2013. Ten lessons for the conservation of African savannah ecosystems. Biological Conservation **167**: 224-232.

Beudels RC, Durant SM, Harwood J. 1992. Assessing the risks of extinction for local populations of Roan antelope *Hippotragus equinus*. Biological Conservation **61**: 107-116.

Bhola N, Ogutu JO, Said MY, Piepho HP, Olff H. 2012. The distribution of large herbivore hotspots in relation to environmental and anthropogenic correlates in the Mara region of Kenya. Journal of Animal Ecology **81**: 1268-1287.

Blank D, Li YM. 2022. Antelope adaptations to counteract overheating and water deficit in arid environments. Journal of Arid Land **14**: 1069-1085.

Bouvet A, Mermoz S, Le Toan T, Villard L, Mathieu R, Naidoo L, Asner GP. 2018. An above-ground biomass map of African savannahs and woodlands at 25 m resolution derived from ALOS PALSAR. Remote Sensing of Environment **206**: 156-173.

Bowkett AE, Rovero F, Marshall AR. 2007. The use of camera-trap data to model habitat use by antelope species in the Udzungwa Mountain forests, Tanzania. African Journal of Ecology **46**: 479-487.

Brashares JS, Arcese P, Sam MK, Coppolillo PB, Sinclair ARE, Balmford A. 2004. Bushmeat hunting, wildlife declines, and fish supply in West Africa. Science **306**: 1180-1183.

Brashares JS, Arcese P, Sam MK. 2001. Human demography and reserve size predict wildlife extinction in West Africa. Proceedings of the Royal Society B **268**: 2473-2478.

Bro-Jørgensen J. 2016. Our antelope heritage, why the fuss? Pages 19-28 in Bro-Jørgensen J, Mallon DP, editors. Antelope conservation: from diagnosis to action. Wiley-Blackwell, London.

Burkepile DE, Burns CE, Tambling CJ, Amendola E, Buis GM, Govender N, Nelson V, Thompson DI, Zinn AD, Smith MD. 2013. Habitat selection by large herbivores in a southern African savanna: the relative roles of bottom-up and top-down forces. Ecosphere **4**: 1-19.

Caro T, Scholte P. 2007. When protection falters. African Journal of Ecology **45**: 233-235.

Castello JR. 2016. Bovids of the world: antelopes, gazelles, cattle, goats, sheep, and relatives. Princeton University Press, Oxford.

Chamaillé-Jammes S, Fritz H, Murindagomo F. 2007. Climate-driven fluctuations in surface-water availability and the buffering role of artificial pumping in an African savanna: potential implication for herbivore dynamics. Austral Ecology **32**: 740-748.

Chardonnet P, Crosmary W. 2013. *Hippotragus equinus*, Roan antelope. Pages 548-556 in Kingdon J, Hoffmann M, editors. Mammals of Africa Volume VI: Hippopotamuses, Pigs, Deer, Giraffe, and Bovids. Bloomsbury, London.

Clegg SB, Turnbull PCB, Foggin CM, Lindeque PM. 2007. Massive outbreak of anthrax in wildlife in the Malilangwe wildlife reserve, Zimbabwe. Veterinary Record **160**: 113-118.

Codron D, Codron J, Lee-Thorp JA, Sponheimer M, Grant CC, Brink JS. 2009. Stable isotope evidence for nutritional stress, competition and loss of functional habitat as factors limiting recovery of rare antelope in southern Africa. Journal of Arid Environments **73**: 449-457.

Cornelis D, Ouedraogo M, Chardonnet P. 2006. Capture et pose de balises Argos sur buffles et hippotragues rouan au parc transfrontalier du W. ECOPAS, Bruxelles.

Courbin N, Loveridg AJ, Macdonald DW, Fritz H, Valeix M, Makuwe ET, Chamaillé-Jammes S. 2016. Reactive responses of zebras to lion encounters shape their predator–prey space game at large scale. Oikos **125**: 829-838.

Craigie ID, Baillie JEM, Balmford A, Carbone C, Collen B, Green RE, Hutton JM. 2010. Large mammal population declines in Africa's protected areas. Biological Conservation **143**: 2221-2228.

Cromsigt JPGM, Prins HHT, Olff H. 2009. Habitat heterogeneity as a driver of ungulate diversity and distribution patterns: interaction of body mass and digestive strategy. Diversity and Distributions **15**: 513-522.

Cutler DC, Edwards TC, Beard KH, Cutler A, Hess KT, Gibson J, Lawler JJ. 2007. Random forests for classification in ecology. Ecology **88**: 2783-2792.

Dagorne D, Kanté A, Rose JB. 2020. A citizen science approach to monitoring of the lion *Panthera leo* (Carnivora: Felidae) population in Niokolo-Koba National Park, Senegal. Journal of Threatened Taxa **12**: 15091-15105.

Daskin JH, Pringle RM. 2018. Warfare and wildlife declines in Africa's protected areas. Nature **553**: 328-332.

Delvingt W, Lobão Tello J. 2004. Découverte du Nord de la Centreafrique sur les terres de la grande faune. ECOFAC. Commission Européenne, Bruxelles.

Di Marco M, Buchanan GM, Szantoi Z, Holmgren M, Marasini GG, Gross D, Tranquilli S, Boitani L, Rondinini C. 2014. Drivers of extinction risk in African mammals: the interplay of distribution state, human pressure, conservation response and species biology. Philosophical Transactions of the Royal Society B **369**: 1-12.

Didan K. 2021. MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SIN Grid V061 [Data set]. Available from https://lpdaac.usgs.gov/products/mod13q1v061/ (accessed March 2023).

Dörgeloh WG, van Hoven W, Rethman NFG. 1996. Population growth of roan antelope under different management systems. South African Journal of Wildlife Research **26**: 113-16.

Dörgeloh WG. 1998. Habitat selection of a roan antelope (*Hippotragus equinus*) population in mixed bushveld, Nylsvlei Nature Reserve. South African Journal of Wildlife Research **28**: 47-57.

Drouilly M, Horion R, Kandji A, Diedhiou LH, Martínez-Martí C, Vernadat F, Ndiaye AA, Henschel P. 2021. Suivi écologique du leopard et des autres espèces à valeur universelle environnementale du Parc National du Niokolo-Koba au Sénégal. République du Sénégal.

Du Toit JT, Owen-Smith N. 1989. Body size, population metabolism, and habitat specialisation among large African herbivores. The American Naturalist **133**: 736-740.

Du Toit JT, Yetman CA. 2005. Effects of body size on the diurnal activity budgets of African browsing ruminants. Behavioural Ecology **143**: 317-325.

East R. 1999. African Antelope Database 1998. IUCN, Cambridge.

Elith J, et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography **29**: 129-151.

Elith J, Leathwick JR. 2009. Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics **40**: 677-697.

El-Sayed A, Kamel M. 2020. Climatic changes and their role in emergence and re-emergence of diseases. Environmental Science and Pollution Research **27**: 22336-22352.

Epaphras AM, et al. 2007. Wildlife water utilization and importance of artificial waterholes during dry season at Ruaha national park, Tanzania. Wetlands Ecology and Management **16**: 183-188.

ESRI. 2022. ArcGIS Pro version 3.0.3. Available from https://pro.arcgis.com/en/pro-app/latest/get-started/get-started.htm (accessed March 2023).

Estes RD, Kingdon J. 2013. Genus *Hippotragus*, Roan and Sable antelopes. Page 547 in Kingdon J, Hoffmann M, editors. Mammals of Africa Volume VI: Hippopotamuses, Pigs, Deer, Giraffe, and Bovids. Bloomsbury, London.

Fick SE, Hijmans RJ. 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. International Journal of Climatology **37**: 4302-4315.

Fiske I, Chandler R. 2011. Unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. Journal of Statistical Software **43**: 1-23.

Fourcade Y, Engler JO, Rödder D, Secondi J. 2014. Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. PLOS One **9**: 1-13.

Franklin J. 1995. Predictive vegetation mapping: geographic modelling of bio-spatial patterns in relation to environmental gradients. Progress in Physical Geography **19**: 474-499.

Fritz H, Loison A. 2006. Large herbivores across biomes. Pages 19-49 in Danell K, Bergström R, Duncan P, Pastor J, editors. Large herbivore ecology, ecosystem dynamics and conservation. Cambridge University Press, Cambridge.

Frost W. 2014. The antelope of Africa. Jacana Media, Johannesburg.

Fryxell JM. 1991. Forage quality and aggregation by large herbivores. The American Naturalist **138**: 478-498.

Fuller A, Mitchell D, Maloney SK, Hetem RS. 2016. Towards a mechanistic understanding of the responses of large terrestrial mammals to heat and aridity associated with climate change. Climate Change Responses **3**: 1-19.

Furstenburg D. 2011. Focus on the roan antelope (*Hippotragus equinus*). S A Hunter **11058**: 36-39.

Galat G, Galat-Luong A, Nizinski JJ, Skovmand O. 2015. Influence of increasing dryness, animal feeding strategy and human hunting on large ungulates abundance: a first approach in West Africa. Russian Journal of Ecology **46**: 71-80.

Gobeyn S, Mouton AM, Cord AF, Kaim A, Volk M, Goethals PLM. 2019. Evolutionary algorithms for species distribution modelling: A review in the context of machine learning. Ecological Modelling **392**: 179-195.

Gómez H, Wallace RB, Ayala G, Tejada R. 2005. Dry season activity periods of some Amazonian mammals. Studies on Neotropical Fauna and Environment **40**: 91-95.

Gonçalves M, Siegismund HR, van Vuuren BJ, Ferrand N, Godinho R. 2021. Evolutionary history of the roan antelope across its African range. Journal of Biogeography **48**: 2812-2827.

Groom R, Harris S. 2010. Factors affecting the distribution patterns of zebra and wildebeest in a resource-stressed environment. African Journal of Ecology **48**: 159-168.

Guillera-Arroita G, Lahoz-Monfort JJ, Elith J, Gordon A, Kujala H, Lentini PE, McCarthy MA, Tingly R, Wintle BA. 2015. Is my species distribution model fit for purpose? Matching data and models to applications. Global Ecology and Biogeography **24**: 276-292.

Guisan A, et al. 2013. Predicting species distribution for conservation decisions. Ecology Letters **16**: 1424-1435.

Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters **8**: 993-1009.

Guisan A, Zimmermann NE. 2000. Predictive habitat distribution models in ecology. Ecological Modelling **135**: 147-186.

Gureja N, Owen-Smith N. 2002. Comparative use of burnt grassland by rare antelope species in a lowveld game ranch, South Africa. South African Journal of Wildlife Research **32**: 31-38.

Hallfors MH, Liao J, Dzurisin J, Grundel R, Hyvarinen M, Towle K, Wu GC, Hellmann JJ. 2016. Addressing potential local adaptation in species distribution models: implications for conservation under climate change. Ecological Applications **26**: 1154-1169.

Harrington R, Owen-Smith N, Viljoen PC, Biggs HC, Mason DR, Funston PJ. 1999. Establishing the cause of the roan antelope decline in the Kruger national park, South Africa. Biological Conservation **90**: 69-78.

Hassanin A, et al. 2012. Pattern and timing of diversification of Cetartiodactyla (*Mammalia, Laurasiatheria*), as revealed by a comprehensive analysis of mitochondrial genomes. Comptes Rendus Biologies **335**: 32-50.

Havemann CP, Retief TA, Collins K, Finn RWS, De Bruyn PJN. 2014. First record of roan antelope (*Hippotragus equinus*) feeding on the fruits of the sausage tree (*Kigelia Africana*). African Journal of Ecology **52**: 568-570.

Havemann CP, Retief TA, Tosh CA, De Bruyn PJN. 2016. Roan antelope *Hippotragus equinus* in Africa: a review of abundance, threats and ecology. Mammal review **46**: 144-158.

Hayward MW, Hayward MD. 2012. Waterhole use by African fauna. South African Journal of Wildlife Research **42**: 117-127.

Heitkönig IMA, Owen-Smith N.1998. Seasonal selection of soil types and grass swards by roan antelope in a South African savanna. African Journal of Ecology **36**: 57-70.

Heitkonig IMA. 1993. Feeding Strategy of Roan Antelope in a Low Nutrient Savanna [PhD Thesis]. University of Witwatersrand, Johannesburg.

Henschel P, Coad L, Burton C, Chataigner B, Dunn A, MacDonald D, Saidu Y, Hunter LTB. 2014. The Lion in West Africa is critically endangered. PLOS ONE **9**: 1-11.

Hensman MC, Owen-Smith N, Parrini F, Erasmus BFN. 2012. Dry season browsing by sable antelope in Northern Botswana. African Journal of Ecology **50**: 513-516.

Hofer H, Campbell KLI, East ML, Huish SA. 1996. The impact of gam meat hunting on target and non-target species in the Serengeti. Pages 117-146 in Taylor VJ, Dunstone N editors. The exploitation of mammal populations. Chapman and Hal, London.

IUCN SSC Antelope Specialist Group. 2017. *Hippotragus equinus*, Roan antelope. Available from https://www.iucnredlist.org/species/10167/50188287 (accessed February 2022).

Jeo RM, Schmidt-Küntzel A, Ballou JD, Sanjayan M. 2018. Drivers of habitat loos and fragmentation: implications for the design of landscape linkages for cheetahs. Pages 137-149 in Nyhus PJ, Marker L, Boast LK, Schmidt-Küntzel A, editors. Cheetahs: biology and conservation. Elsevier, Amsterdam.

Kaiser FK, De le Roi M, Mirolo M, Jesse ST, Puff C, Bohner J, Ludlow M, Baumgärtner W, Osterhaus A. 2023. Evidence for a novel gammaherpesvirus as the putative agent of malignant catarrhal fever disease in roan antelopes (*Hippotragus equinus*). Viruses **15**: 1-10.

Kark S. 2013. Effects of ecotones on biodiversity. Pages 142-148 in Levin SA, editors. Encyclopedia of Biodiversity. Elsevier Academic Press, Amsterdam.

Kasiringua E, Kopij G, Proches S. 2017. Daily activity patterns of ungulates at water holes during the dry season in the Waterberg National Park, Namibia. Russian Journal of Theriology **16**: 129-138.

Kay RNB. 1997. Responses of African livestock and wild herbivores to drought. Journal of Arid Environments **37**: 683-694.

Kimanzi JK, Sanderson RA, Rushton SP, Mugo MJ. 2015. Spatial distribution of snares in Ruma national park, Kenya, with implications for management of the roan antelope *Hippotragus equinus langheldi* and other wildlife. Oryx **49**: 295-302.

Kimanzi JK, Sanderson RA, Rushton SP. 2013. Habitat suitability modelling and implications for management of roan antelopes in Kenya. African Journal of Ecology **52**: 111-121.

Kingdon J. 1982. East African mammals: an atlas of evolution in Africa. Academic Press, London.

Kingdon J. 2015. The Kingdon field guide to African mammals: Second edition. Bloomsbury Publishing, London.

Klop E, Goethem J, De Jongh HH. 2007. Resource selection by grazing herbivores on post-fire regrowth in a West African woodland savanna. Wildlife Research **34**: 77-83.

Knight M. 2013. *Oryx gazella*, Gemsbok (Southern Oryx). Pages 572-576 571 in Kingdon J, Hoffmann M, editors. Mammals of Africa Volume VI: Hippopotamuses, Pigs, Deer, Giraffe, and Bovids. Bloomsbury, London.

Knight MH, Novellie P, Holness S, Du Toit J, Ferreira S, Hofmyr M, Grant C, Herbst M, Gaylard A. 2016. Hands-on approaches to managing antelopes and their ecosystems: a South African perspective. Pages 137-161 in Bro-Jørgensen J, Mallon DP, editors. Antelope conservation: from diagnosis to action. Wiley-Blackwell, London.

Knoop MC, Owen-Smith N. 2006. Foraging ecology of roan antelope: key resources during critical periods. African Journal of Ecology **44**: 228–236.

Kovach WL. 2011. Oriana–circular statistics for windows, ver. 4. Kovach Computing Services, Pentraeth.

Lahoz-Monfort JJ, Guillera-Arroita G, Wintle BA. 2014. Imperfect detection impacts the performance of species distribution models. Global Ecology and Biogeography **23**: 504-515.

Laundré JW. 2010. Behavioural response races, predator-prey shell games, ecology of fear, and patch use of pumas and their ungulate prey. Ecology **91**: 2995-3007.

Lissozsky AA, Dudov SV, Obolenskaya EV. 2021. Species-distribution modelling: advantages and limitations of its application. 1. general approaches. Biology Bulletin Reviews **11**: 254-264.

Loarie SR, Tambling CJ, Asner GP. 2013. Lion hunting behaviour and vegetation structure in an African savanna. Animal Behaviour **85**: 899-906.

Mariotti E, Parrini F, Louw CJ, Marshal JP. 2020. Habitat use by a large herbivore guild in a fenced South African protected area. African Journal of Wildlife Research **50**: 86-101.

Martin J, Owen-Smith S. 2016. Habitat selectivity influences the reactive responses of African ungulates to encounters with lions. Animal Behaviour **116**: 163-170.

Martinez-Minaya J, Cameletti M, Conesa D, Pennino MG. 2018. Species distribution modeling: a statistical review with focus in spatio-temporal issues. Stochastic Environmental Research and Risk Assessment **32**:3227-3244.

Masih I, Maskey S, Mussá FEF, Trambauer P. 2014. A review of droughts on the African continent: a geospatial and long-term perspective. Hydrology and Earth System Sciences **18**: 3635-3649.

McGrew WC, Baldwin PJ, Marchant LF, Pruetz JD, Tutin CEG. 2014. Chimpanzees (*Pan troglodytes verus*) and their mammalian sympatriates: Mt. Assirik, Niokolo-Koba National Park, Senegal. Primates **55**: 525-532.

Mcloughin CA, Owen-Smith N. 2003. Viability of a diminishing roan antelope population: predation is the threat. Animal Conservation **6**: 231-236.

Miller J. 2010. Species distribution modelling. Geography Compass **4**: 490-509.

Muposhi VK, Gandiwa E, Chemura A, Bartels P, Makuza SM, Madiri TH. 2016. Habitat heterogeneity variably influences habitat selection by wild herbivores in a semi-arid tropical savanna ecosystem. PLoS One **11**: 1-24.

NASA JPL. 2013. NASA Shuttle Radar Topography Mission Global 1 arc second. Available from https://lpdaac.usgs.gov/products/srtmgl1v003/ (accessed March 2023).

Newby J. 2013. *Addax nasomaculatus*, Addax. Pages 566-571 in Kingdon J, Hoffmann M, editors. Mammals of Africa Volume VI: Hippopotamuses, Pigs, Deer, Giraffe, and Bovids. Bloomsbury, London.

Newmark WD. 2008. Isolation of African protected areas. Frontiers in Ecology and the Environment **6**: 321-328.

Nieman WA, Van Wilgen BW, Leslie AJ. 2021. A review of fire management practices in African savanna-protected areas. African Protected Area Conservation and Science **63**: 1-13.

Ostfeld RS. 2009. Climate change and the distribution and intensity of infectious diseases. Ecology **90**: 903-905.

Owen-Smith N, Goodall V. 2014. Coping with savanna seasonality: comparative daily activity patterns of African ungulates as revealed by GPS telemetry. Journal of Zoology **293**: 181-191.

Owen-Smith N, Hopcraft G, Morrison T, Chamaillé-Jammes S, Hetem R, Bennitt E, Van Langevelde F. 2020. Movement ecology of large herbivores in African savannas: current knowledge and gaps. Mammal Review **50**: 252-266.

Owen-Smith N. 2013. *Tragelaphus strepsiceros*, Greater Kudu. Pages 152-159 in Kingdon J, Hoffmann M, editors. Mammals of Africa Volume VI: Hippopotamuses, Pigs, Deer, Giraffe, and Bovids. Bloomsbury, London.

Owen-Smith N. 2019. Ramifying effects of the risk of predation on African multi-predator, multi-prey large-mammal assemblages and the conservation implications. Biological Conservation **232**: 51-58.

Perrin MR, Taolo C. 1998. Home range, activity pattern and social structure of an introduced herd of roan antelope in KwaZulu-Natal, South Africa. South African Journal of Wildlife Research **28**: 27-32.

Perrin MR, Taolo CL. 1999. Diet of introduced roan antelope at Weenen nature reserve, South Africa. South African Journal of Wildlife Research **29**: 43-51.

Peterson AT, Papeş M, Soberón J. 2015. Mechanistic and correlative models of ecological niches. European Journal of Ecology **1**: 28-38.

Pettorelli N, Ryan S, Mueller T, Bunnefeld N, Je Drzejewska B, Lima M, Kausrud K. 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate Research **46**: 15-27.

Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modelling of species geographic distributions. Ecological Modelling **190**: 231-259.

Poche RM. 1974. Notes on the Roan antelope (*Hippotragus equinus* (Desmarest)) in West Africa. Journal of Applied Ecology **11**: 963-968.

Price MRS. 2016. Reintroduction as an antelope conservation solution. Pages 217-252 in Bro-Jørgensen J, Mallon DP, editors. Antelope conservation: from diagnosis to action. Wiley-Blackwell, London.

Qazi AW, Saqib Z, Zama-ul-Haq M. 2022. Trends in species distribution modelling in context of rare and endemic plants: a systematic review. Ecological Processes **11**: 1-11.

Rabeil T, Hejcmanová P, Gueye M, Greffrath R, Cornut D. 2018. Inventaire combiné terrestre et aérien: Parc National du Niokolo-Koba, Sénégal. République du Sénégal.

Redfern JV, Grant R, Biggs H, Getz WM. 2003. Surface-water constraints on herbivore foraging in the Kruger national park, South Africa. Ecology **84**: 2092-2107.

Renaud PC, Gueye MB, Hejcmanová P, Antoninova M, Samb M. 2006. Inventaire aérien et terrestre de la faune et relevé des pressions au Parc National du Niokolo Koba. République du Sénégal.

Reside AE, Watson I, VanDerWal J, Kutt AS. 2011. Incorporating low-resolution historic species location data decreases performance of distribution models. Ecological Modelling **222**: 3444-3448.

Riginos C, Grace JB. 2008. Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. Ecology **89**: 2228-2238.

Ripple WJ, et al. 2015. Collapse of the world’s largest herbivores. Science Advances **1**: 1-12.

RStudio Team (2022). RStudio: Integrated Development Environment for R. RStudio, PBC, Boston. Available from http://www.rstudio.com/ (accessed October 2022).

Schertler A, Rabitsch W, Moser D, Wessely J, Essl F. 2020. The potential current distribution of the coypu (*Myocastor coypus*) in Europe and climate change induced shifts in the near future. Neobiota **58**: 129-160.

Scholte P, Adam S, Serge BK. 2007. Population trends of antelopes in Waza national park (Cameroon) from 1960 to 2001: the interacting effects of rainfall, flooding and human interventions. African Journal of Ecology **45**: 431-439.

Scholte P. 2011. Towards understanding large mammals population declines in Africa’s protected areas: a West-Central African perspective. Tropical Conservation Science **4**: 1-11.

Schuette JR, Leslie DM, Lochmiller RL, Jenks JA. 1998. Diest of Hartebeest and Roan antelope in Burkina Faso: support of the long-faced hypothesis. Journal of Mammalogy **79**: 426-436.

Sinclair ARE, Mduma S, Brashares JS. 2003. Patterns of predation in a diverse predator–prey system. Nature **425**: 288-290.

Sinclair ARE. 1985. Does interspecific competition or predation Shape the African ungulate community? Journal of Animal Ecology **54**: 899-918.

Sinibaldi I, Schmidt K, Scholte P, Van Duren IC, Corsi F, Brouwer J, Prins HHT. 2004. Dependence of large mammals in sub-Saharan Africa on water and water management: report to the WWF. Wagenigen University and Research Centre, Wagenigen.

Sintayehu DW. 2018. Impact of climate change on biodiversity and associated key ecosystem services in Africa: a systematic review. Ecosystem Health and Sustainability **4**: 225-239.

Smit IPJ, Grant CC, Devereux BJ. 2007. Do artificial waterholes influence the way herbivores use the landscape ? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. Biological Conservation **136**: 85-99.

Steyl JCA, Prozesky L, Stoltsz WH, Lawrence JA. 2012. Theileriosis (*Cytauxzoonosis*) in roan antelope (*Hippotragus equinus*): field exposure to infection and identification of potential vectors. Onderstepoort Journal of Veterinary Research **79**: 1-8.

Thaker M, Vanak AT, Owen CR, Ogden MB, Niemann SM, Slotow R. 2011. Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. Ecology **92**: 398-407.

Thuiller W, et al. 2008. Predicting global change impact on plant species' distribution: future challenges. Perspectives in Plant Ecology, Evolution and Systematics **9**: 137-152.

Tourinho L, Vale MM. 2023. Choosing among correlative, mechanistic, and hybrid models of species' niche and distribution. Integrative Zoology **18**: 93-109.

Traill LW. 2004. Seasonal utilization of habitat by large grazing herbivores in semi-arid Zimbabwe. South African Journal of Wildlife Research **34**: 13-24.

Treydte AC, Grant CC, Jeltsch F. 2009. Tree size and herbivory determine below-canopy grass quality and species composition in savannahs. Biodiversity and Conservation **18**: 3989-4002.

Tucker MA, Bohring-Gaese K, Fagen WF, Fryxell JM, Van Moorter B, Alberts SC. 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. Science **359**: 466-469.

Tyowua BT, Agblusi EA, Orsar JT. 2013. Roan antelope (*Hippotragus equinus*, Desmarest 1804 food plants and feeding habits in the Kainji lake national park, Nigeria. Journal of Research in Forestry, Wildlife and Environment **4**: 22-29.

Tyowua BT, Orsar JT, Agbelusi EA. 2012a. Habitat preference of Roan antelope (*Hippotragus equinus*, Desmarest 1804) in Kainji lake national park, Nigeria. International Research Journal of Agricultural Science and Soil Science **2**: 421-425.

Tyowua BT, Orsar JT, Agbelusi EA. 2012b. Seasonal variation in herd size of roan antelope (*Hippotragus equinus*, Desmarest 1804) in Kainji lake national park, Nigeria. Global Advanced Research Journal of Environmental Science and Toxicology **1**: 110-114.

UNSECO. 2023. Niokolo-Koba National Park. UNESCO, Senegal. Available from https://whc.unesco.org/en/list/153/ (accessed January 2023).

Van Beest FM, Rivrud IM, Loe LE, Milner JM, Mysterud A. 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? Journal of Animal Ecology **80**: 771-785.

Veldhuis MP, Kihwele ES, Cromsigt JPGM, Ogutu JO, Hopcraft JGC, Owen-Smith N, Olff H. 2019. Large herbivore assemblages in a changing climate: incorporating water dependence and thermoregulation. Ecology Letters **22**: 1536-1546.

Vinks MA, et al. 2020. Testing the effects of anthropogenic pressures on a diverse African herbivore community. Ecosphere **11**: 1-22.

Watson FGR, Becker MS, Milanzi J, Nyir-Enda M. 2014. Human encroachment into protected area networks in Zambia: implications for large carnivore conservation. Regional Environmental Change **15**: 415-429.

Wilson DE, Bartsch RC, Bigalke RD, Thomas SE. 1974. Observations on mortality rates and disease in roan and sable antelope on nature reserves in the Transvaal. Journal of the Southern African Wildlife Management Association **4**: 203-206.

Wilson DE, Hirst S. 1977. Ecology and factors limiting roan and sable antelope populations in South Africa. Wildlife Monographs **54**: 1-109.

Wirsing AJ, Cameron KE, Heithaus MR. 2010. Spatial responses to predators vary with prey escape mode. Animal Behaviour **79**: 531-537.

Wisz MS, Hijmans RJ, Li J, Petrson AT, Graham CH, Guisan A. 2008. Effects of sample size on the performance of species distribution models. Diversity and Distributions **14**: 763-773.

Wittemyer G, Elsen P, Bean WT, Burton ACO, Brashares JS. 2008. Accelerated human population growth at protected area edges. Science **321**: 123-126.

Wu M, Schurgers G, Rummukainen M, Smith B, Samuelsson P, Jansson C, Siltberg J, May W. 2016. Vegetation–climate feedbacks modulate rainfall patterns in Africa under future climate change. Earth System Dynamics **7**: 627-647.

Yiu SW, Owen-Smith N, Cain JW. 2022. How lions move at night when they hunt? Journal of Mammalogy **103**: 855-864.

Young C, Fritz H, Smithwick E, Venter JA. 2020. The landscape-scale drivers of herbivore assemblage distribution on the central basalt plains of Kruger national park. Journal of Tropical Ecology **36**: 13-28.

Yu H, Cooper AR, Infante DM. 2020. Improving species distribution model predictive accuracy using species abundance: application with boosted regression trees. Ecological Modelling **432**: 1-11.

Appendices

List of the Appendices

Appendix 1: R code created for modelling

Appendix 2: Raster outputs of all environmental variables

Appendix 1: R code created for modelling

```
######################  SDM Roan Unmarked ##############################
#########################################################################

setwd("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM")
getwd()

rm(list=ls());gc() #clear environment

 install.packages("camtrapR")
 install.packages("unmarked")
 install.packages("ggplot2")
 install.packages("rgdal")
 install.packages("plotKML")
 install.packages("Hmisc")
 install.packages("corrplot")
 install.packages("MuMIn")
 install.packages("rasterVis")
 install.packages("lattice")

  library(camtrapR)
  library(unmarked)
  library(ggplot2)
  library(rgdal)
  library(plotKML)
  library(Hmisc)
  library(corrplot)
  library(MuMIn)
  library(raster)
  library(sp)
  library(sf)
  library(tidyverse)
  library(lattice)
  library(rasterVis)
  library(latticeExtra)

##################################################################
################  Species Data Preparation ######################
##################################################################

camera_data <- read.csv("CT_nknp.csv", sep = ',')
#str(camera_data)
camera_data$Date_set = as.Date(camera_data$Date_set,"%d/%m/%Y")
camera_data$Date_retrieved = as.Date(camera_data$Date_retrieved,"%d/%m/%Y")
camera_data$Problem1_from = as.Date(camera_data$Problem1_from,"%d/%m/%Y")
camera_data$Problem1_to = as.Date(camera_data$Problem1_to,"%d/%m/%Y")
camera_data$Problem2_from = as.Date(camera_data$Problem2_from, "%d/%m/%Y")
camera_data$Problem2_to = as.Date(camera_data$Problem2_to, "%d/%m/%Y")

 ## Troublshooting operational problems with camera


camop_problem <- cameraOperation( CTtable = camera_data,
                                   cameraCol = "CameraID",
                                  setupCol = "Date_set",
                                  retrievalCol = "Date_retrieved",
                                  writecsv = FALSE ,
                                  hasProblems = TRUE,
```

```
                                   byCamera = FALSE,
                                   allCamsOn = FALSE,
                                   camerasIndependent = FALSE,
                                   dateFormat = "%Y-%m-%d" )

## Looking at the number of events of Roan

 #rm(roan_events)
 roan_events <- read.csv("Roan_CTevents.csv")

roan_events$Date = as.Date(roan_events$Date,"%d/%m/%Y")
roan_events$timestamp = as.POSIXct(as.POSIXct(paste(roan_events$Date,
roan_events$Time),
                                             format= "%Y-%m-%d %H:%M:%S"
 ))
 head(roan_events)
 #str(roan_events)
 #head(roan_events)

nrow(roan_events) # how many events I have of Roan

# creating a report to summarise all the information above

Report <- surveyReport(recordTable = roan_events,
                       CTtable = camera_data,
                       stationCol = "Station",
                        cameraCol = "CameraID",
                        setupCol = "Date_set",
                        retrievalCol = "Date_retrieved",
                        CTDateFormat = "%Y-%m-%d",
                        CTHasProblems = TRUE,
                        recordDateTimeCol = "timestamp"
 )
 str(Report)

  Report_ebs <- Report$events_by_species
  Report_ebs
  write.csv(Report_ebs, "eventbyspecies.csv")

  Report_surveydates <- Report$survey_dates
  Report_surveydates
  write.csv(Report_surveydates, "surverydates.csv")

  Report_bystation <- Report$events_by_station
  Report_bystation
  write.csv(Report_bystation, "eventsbystation.csv")

  ## detection history matrix was created manually under the name:
  ## Roan_detection_history.csv

  ######################################################################
  ############  Environmental Data Preparation ########################
  #####################################################################

  Envi_var <- read.csv("Envi_stations.csv")
  covariates <- Envi_var[, 5:16]
  summary(covariates[,1:12])
  write.csv(summary(covariates[, 1:12]), "cov_summary.csv")

 ## run a correlation matrix using Pearson's, to be able to visualise which
 ## environmental variables are strongly correlated and should therefore be
 ## removed to not compromise model function
```

```
## this is for P-values of correlation matrix

correlation_envi <- rcorr(as.matrix(covariates),
                          type = c("pearson"))
correlation_envi

## this is for the Pearson correlation coefficient values

corr <- cor(covariates)
round(corr, 2)

corrplot(corr,
         method = c("circle"),
         type = c("upper"),
         order = c("hclust"),
         tl.col = "black",
         tl.srt = 25
                      )
corrplot(corr,
         method = c("circle"),
         type = c("upper"),
         order = c("FPC"),
         tl.col = "black",
         tl.srt = 40,
         tl.pos = 'full',
         mar = c(1,1,1,1)
)
corrplot(corr,
         add = TRUE,
         type = 'lower',
         method = 'number',
         order = 'FPC',
         diag = FALSE,
         tl.pos = 'n',
         cl.pos = 'n',
         mar = c(1,1,1,1),
         number.cex = 0.5,
         number.font = 1,
)
## Standardising all environmental variables

covariates$DEMx = scale(covariates$DEM)
covariates$SLOPEx = scale(covariates$SLOPE)
covariates$DistRivx = scale(covariates$DistRiv)
covariates$DistMarx = scale(covariates$DistMar)
covariates$NDVIx = scale(covariates$NDVI)
covariates$NDVI_SDx = scale(covariates$NDVI_SD)
covariates$AGBx = scale(covariates$AGB)
covariates$bio1x = scale(covariates$bio1)
covariates$bio4x = scale(covariates$bio4)
covariates$bio5x = scale(covariates$bio5)
covariates$bio12x = scale(covariates$bio12)
covariates$bio15x = scale(covariates$bio15)

for (i in 1:length(covariates)) {
  covariates[[i]] <- scale(covariates[[i]])
}

covariates_scaled <- covariates[,-1:-12]
```

```
 ## Elimination of the highly correlated environmental variables
 ## All_covariates: Removal of DistRiv, Bio5 and Bio12 AND bio15

 All_covariates <- covariates_scaled[, -10: -12]
 All_covariates <- All_covariates[, -3]

 ######################################################################
 #################  Roan occupancy modelling  #######################
 ######################################################################

 det_roan <- read.csv("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/
 Roan_detection_history.csv")

##remove station

 detsRoan <- det_roan[, -1]
 UFO_Roan <- unmarkedFrameOccu(y=detsRoan)
 summary(UFO_Roan)

 ## include scaled covariates into occupancy frame (first All_covariates)

 UFOAllcov_Roan <- unmarkedFrameOccu(y=detsRoan, siteCovs = All_covariates)
 summary(UFOAllcov_Roan)

 ######################## Run the models ##############################
 ## Model 1 (m1) includes no covariates at all so detection probability and
 ##occupancy are unvarying/consistent
 ## psi = occupancy probability, and p= detection probability

 m1 <- occu(~1 ~1, data = UFOAllcov_Roan)
 m1
 ## backtransform so probabilities are proportionate to better understand
 m1.psi <- backTransform(m1, type= "state")
 m1.psi

 m1.p <- backTransform(m1, type= "det")
 m1.p
 ## this tells us that Roan occurs at 63% of sites taking into account
 imperfect
 ##detection AND that we have a 6% chance of detection Roan when they are
 there
 ## calculate 95% confidence interval for both occupancy and detection
 probability

 m1CI.psi <- confint(m1.psi)
 m1CI.psi

 m1CI.p <- confint(m1.p)
 m1CI.p

## models 2-9 are run with individual variables

 m2 <- occu(~1 ~DEMx, data = UFOAllcov_Roan)
 m2

 m3 <- occu(~1 ~SLOPEx, data = UFOAllcov_Roan)
 m3

 m4 <- occu(~1 ~DistMarx, data = UFOAllcov_Roan)
 m4
```

```
 m5 <- occu(~1 ~NDVIx, data = UFOAllcov_Roan)
 m5

 m6 <- occu(~1 ~NDVI_SDx, data = UFOAllcov_Roan)
 m6

m7 <- occu(~1 ~AGBx, data = UFOAllcov_Roan)
m7

m8 <- occu(~1 ~bio1x, data = UFOAllcov_Roan)
m8

m9 <- occu(~1 ~bio4x, data = UFOAllcov_Roan)
m9

# m10 is model with all environmental values

  m10 <- occu(~1 ~DEMx + SLOPEx + DistMarx + NDVIx + NDVI_SDx + AGBx + bio1x
  + bio4x, data = UFOAllcov_Roan)
  m10

  ## the next few models are exploratory combinations

  m11 <- occu(~1 ~AGBx + NDVIx, data = UFOAllcov_Roan)
  m11

 m12 <- occu(~1 ~DistMarx + bio4x, data = UFOAllcov_Roan)
 m12

 m13 <- occu(~1 ~DEMx + AGBx, data = UFOAllcov_Roan)
 m13

 m14 <- occu(~1 ~AGBx + DistMarx + bio4x, data = UFOAllcov_Roan)
 m14

fit_roan <- fitList('psi(.)p(.)' = m1,
                    'psi(DEMx)p(.)' = m2,
                    'psi(SLOPEx)p(.)' = m3,
                    'psi(DistMarx)p(.)' = m4,
                    'psi(NDVIx)p(.)' = m5,
                    'psi(NDVI_SDx)p(.)' = m6,
                    'psi(AGBx)p(.)' = m7,
                    'psi(bio1x)p(.)' = m8,
                    'psi(bio4x)p(.)' = m9,
                    'psi(DEMx + SLOPEx + DistMarx + NDVIx + NDVI_SDx + AGBx
+ bio1x + bio4x)p(.)' = m10,
                    'psi(AGBx + NDVIx)p(.)' = m11,
                    'psi(DistMarx + bio4x)p(.)' = m12,
                    'psi(DEMx + AGBx)p(.)' = m13,
                    'psi(AGBx + DistMarx + bio4x)p(.)' = m14
)
 modSel(fit_roan)
 fit_roan

## use Dredge function to look at all the possible models for each cov
sections
 ## first for all
 All_cov <- occu(formula = ~1 ~DEMx + SLOPEx + DistMarx + NDVIx + NDVI_SDx +
                    AGBx + bio1x + bio4x,
                data = UFOAllcov_Roan)
  Allmodellist <- dredge(All_cov,
                         rank = "AIC")
```

```
write.csv(Allmodellist, "Allmodelllist.csv")

## looking at all the delta values and model options, it seems like the
most
## explanatory is using only AGB as a variable, so run individual model on
it
## also backtransform to be able to interpret although this is also done in
## the predictions

backTransform(linearComb(m7, coefficients = c(1,0), "state"))
##################################################################
###########  Occupancy prediction NKNP ###########################
#################################################################
## preparation of raster data

DEM <- raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/DEM/
DEM.tif")
Slope <- raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/
Slope_30m/Slope.tif")
DistMar <- raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/
Dist_Mare_50m/DistMare_nk.tif")
NDVI <- raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/
NDVI_250m/NDVI.tif")
NDVI_sd <- raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/
NDVI_sd_250m/NDVI_sd.tif")
AGB <- raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/AGB_50m/
AGB_nk.tif")
bio1 <- raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/bio1/
bio1.tif")
bio4 <- raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/bio4/
bio4.tif")

DistRiv <- raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/
Dist_River_50m/DistRiver_nk.tif")
bio5 <- raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/bio5/
bio5.tif")
bio12 <- raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/bio12/
bio12.tif")
bio15 <- raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/bio15/
bio15.tif")


png("bio15plot.png", width = 800, height = 600, units = "px")
dev.off()

plot(DEM)
plot(Slope)
plot(DistMar)
plot(NDVI)
plot(NDVI_sd)
plot(AGB)
plot(bio1)
plot(bio4)

plot(DistRiv)
plot(bio5)
plot(bio12)
plot(bio15)
## important to make them the same extent and resolution before stacking
them
```

```r
## we will do one for just environmental (50m resolution)
## one for just climatic (1km resolution)
## and one for 'all' which does not include bio15 at also 50m resolution?
## Make sure the layer you are using for your model extent and resolution
is the
## first one you write in the list otherwise you will cry for at least an
hour

rm(Envi_rasters)
Envi_rasters <- list(AGB, DistMar, DEM, Slope, NDVI, NDVI_sd, bio1, bio4)
for (i in 2:length(Envi_rasters)) {
  Envi_rasters[[i]] <- resample(Envi_rasters[[i]], AGB)
}
rm(Envi_s)
Envi_s <- stack(Envi_rasters)
Envi_s

Envi_nknp <- as.data.frame(rasterToPoints( Envi_s ), xy = TRUE )
str(Envi_nknp)
summary(Envi_nknp)
write.csv(Envi_nknp, "EnviNKNP.csv")

## same as before, standardise the variables in your raster stack

Envi_nknp$AGBx = scale(Envi_nknp$AGB_nk)
Envi_nknp$DistMarx = scale(Envi_nknp$DistMare_nk)
Envi_nknp$DEMx = scale(Envi_nknp$DEM)
Envi_nknp$Slopex = scale(Envi_nknp$Slope)
Envi_nknp$NDVIx = scale(Envi_nknp$NDVI)
Envi_nknp$NDVI_sdx = scale(Envi_nknp$NDVI_sd)
Envi_nknp$bio1x = scale(Envi_nknp$Band_1.1)
Envi_nknp$bio4x = scale(Envi_nknp$Band_1.2)

## predict using AGB model

PredRoanm7 <- predict(m7,
                      type = "state",
                      newdata = Envi_nknp,
                      na.rm = TRUE,
                      inf.rm = TRUE)

Roanm7 <- levelplot(Predicted ~ Envi_nknp$x + Envi_nknp$y,
                    data = PredRoanm7,
                    col.regions = rev(terrain.colors(100)),
                    at = seq(0,1,length.out=101),
                    scales = list(y = list(relation = "free")))

Roanm7

## statistical evaluation of prediction

fitstats <- function(m7,
                     method = "nonparboot") {
  observed <- getY(m7@data)
  expected <- fitted(m7)
  resids <- residuals(m7,method = "nonparboot")
```

```
sse <- sum(resids^2,na.rm = TRUE)
chisq <- sum((observed - expected)^2 / expected,na.rm = TRUE)
freeTuke <- sum((sqrt(observed) - sqrt(expected))^2,na.rm = TRUE)

out <- c(SSE = sse,
             Chisq = chisq,
             freemanTukey = freeTuke)
   return(out)
 }

 pb <- parboot(m7,
               fitstats,
               nsim = 1000,
               report = TRUE,
               method = "nonparboot")
 pb

 par(mfrow = c(3,1))

 ## now do the same for AGB prediction in the AOI

  DEM_AOI <- raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/
  AOI_rasters/DEM//dem/DEM.tif")
  Slope_AOI <- raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/
  AOI_rasters/Slope/slope/Slope.tif")
  DistMar_AOI <-  raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/
  AOI_rasters/DistMar/mar/Mar.tif")
  NDVI_AOI <-  raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/
  AOI_rasters/NDVI/ndvi//NDVI.tif")
  NDVI_SD_AOI <- raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/
  AOI_rasters/NDVI_SD/ndvi_sd/NDVI_SD.tif")
  AGB_AOI <- raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/
  AOI_rasters/AGB/agb/AGB.tif")
  bio1_AOI <- raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/
  AOI_rasters/bio1//bio1/bio1.tif")
  bio4_AOI <- raster("C:/Users/Thalia Pelegrin/Desktop/Roan_SDM/Rasters/
  AOI_rasters//bio4/bio4/bio4.tif")
  AOI_rasters <- list(DistMar_AOI, DEM_AOI, Slope_AOI, NDVI_AOI, NDVI_SD_AOI,
  bio1_AOI, bio4_AOI, AGB_AOI)
  for (i in 2:length(AOI_rasters)) {
    AOI_rasters[[i]] <- resample(AOI_rasters[[i]], DistMar_AOI)
  }


   AOI_stack <- stack(AOI_rasters)
   AOI_stack

   Envi_AOI <- as.data.frame(rasterToPoints( AOI_stack ), xy = TRUE )
   str(Envi_AOI)
   summary(Envi_AOI)
   write.csv(Envi_AOI, "EnviAOI.csv")

  Envi_AOI$AGBx = scale(Envi_AOI$AGB)
  Envi_AOI$DistMarx = scale(Envi_AOI$Mar)
  Envi_AOI$DEMx = scale(Envi_AOI$DEM)
  Envi_AOI$Slopex = scale(Envi_AOI$Slope)
  Envi_AOI$NDVIx = scale(Envi_AOI$NDVI)
  Envi_AOI$NDVI_sdx = scale(Envi_AOI$NDVI_SD)
```

```
Envi_AOI$bio1x = scale(Envi_AOI$bio1)
Envi_AOI$bio4x = scale(Envi_AOI$bio4)

PredRoanm7_AOI <- predict(m7,
                          type = "state",
                          newdata = Envi_AOI,
                          na.rm = TRUE,
                          inf.rm = TRUE)

Roanm7_AOI <- levelplot(Predicted ~ Envi_AOI$x + Envi_AOI$y,
                        data = PredRoanm7_AOI,
                        col.regions = rev(terrain.colors(100)),
                        at = seq(0,1,length.out=101),
                        scales = list(y = list(relation = "free")))

Roanm7_AOI
```

RoanSDM.pdf

Appendix 2: Raster outputs of all environmental variables

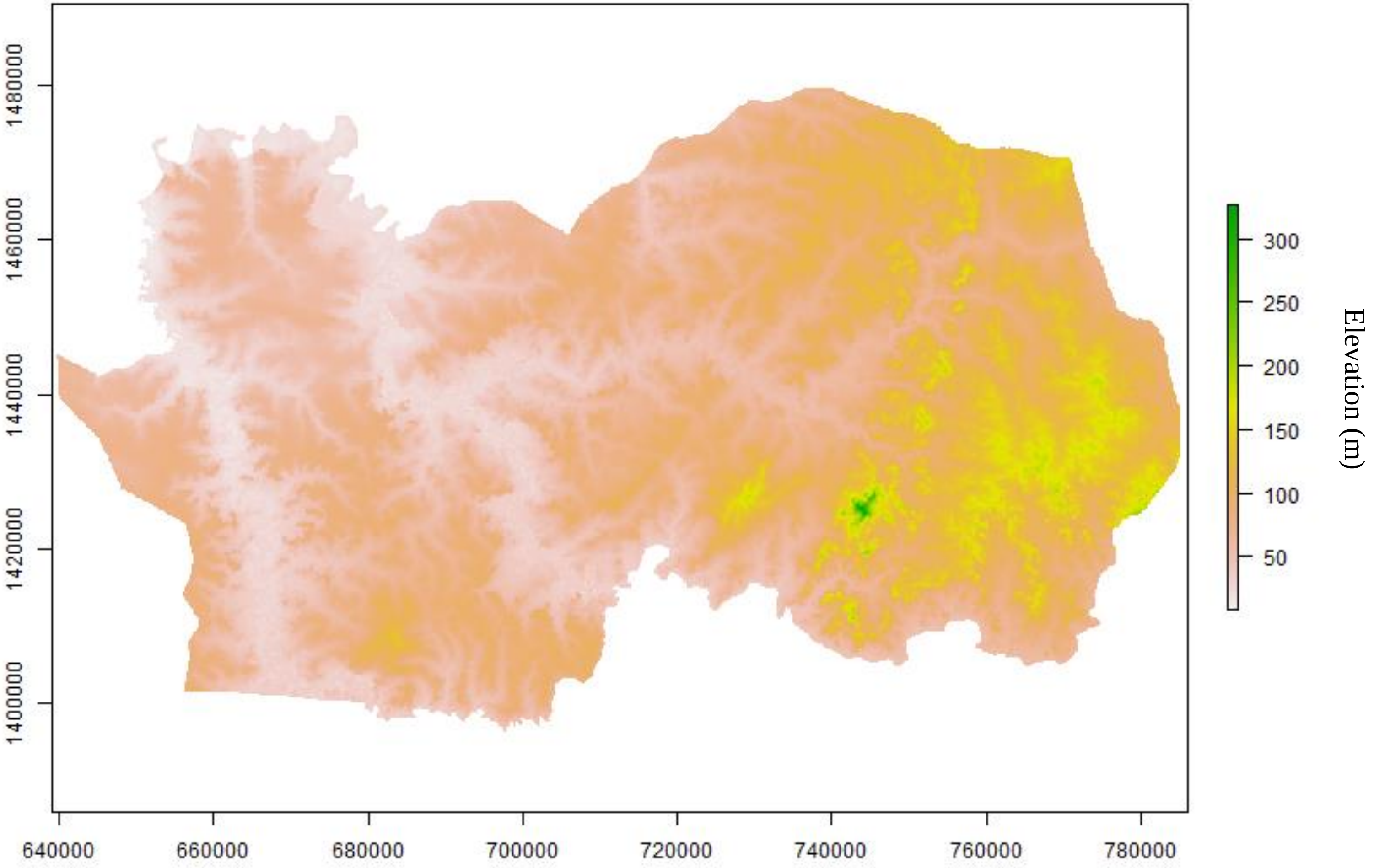


Figure 19: DEM raster

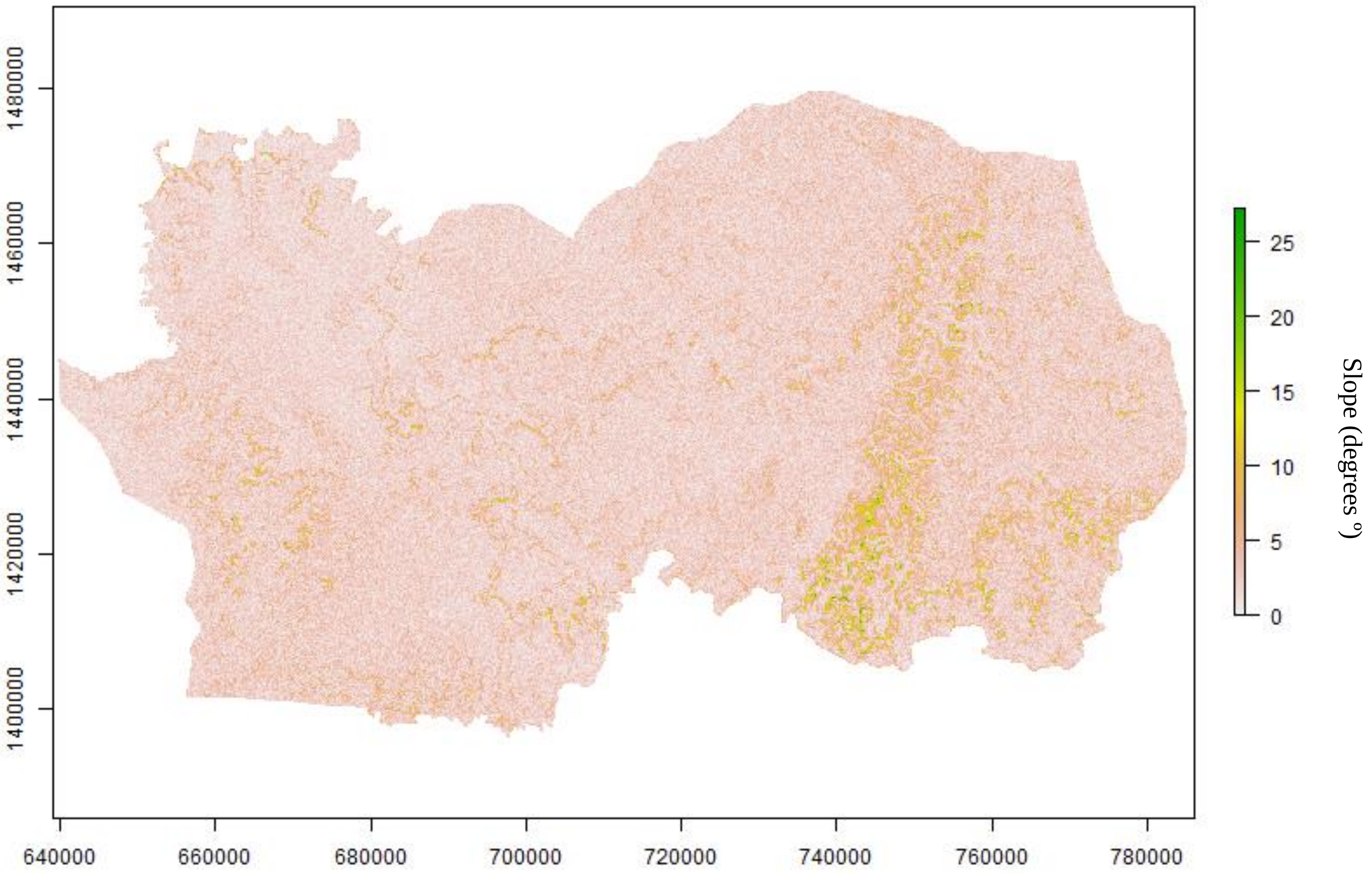


Figure 20: Slope raster

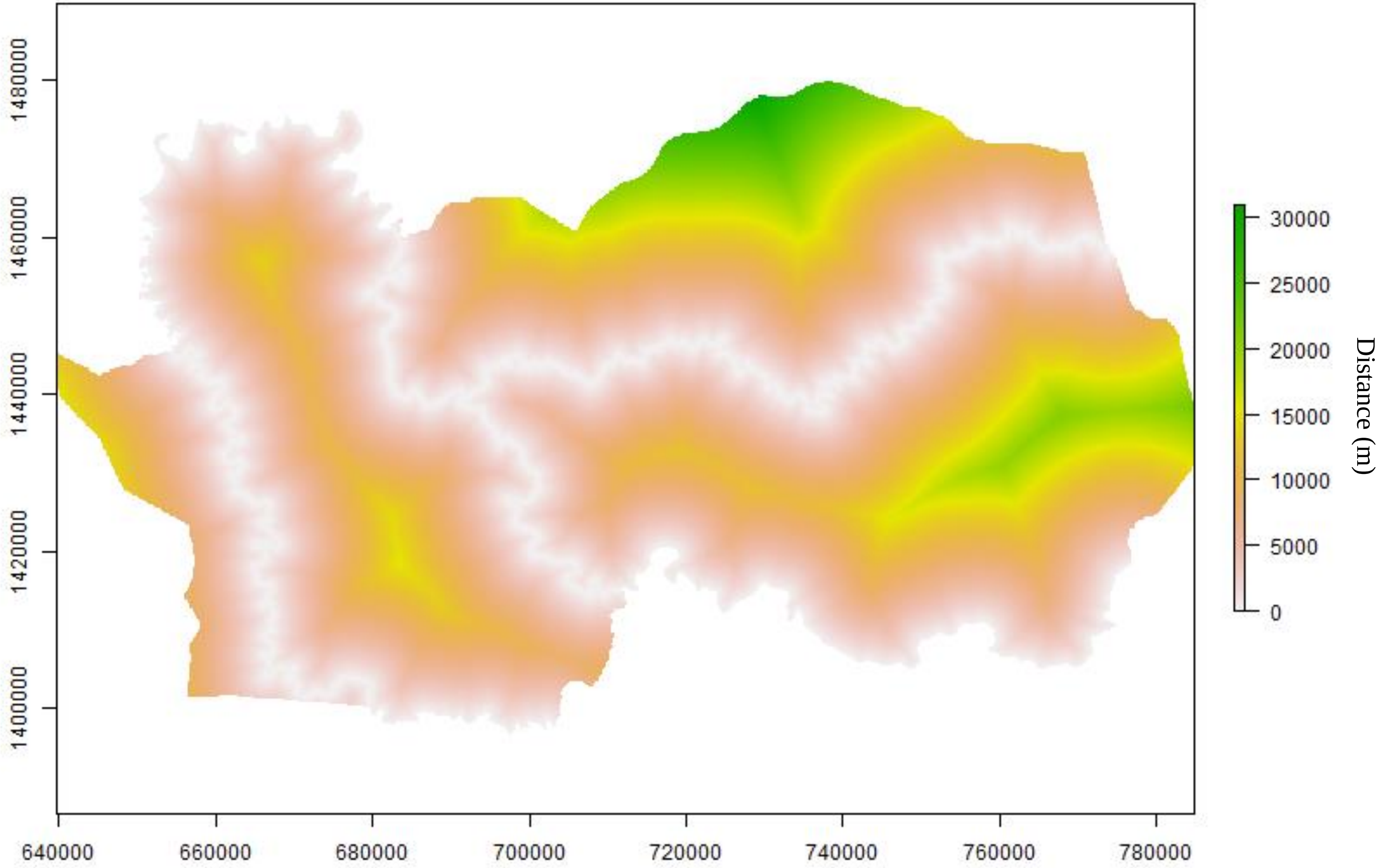


Figure 21: DistRiv raster

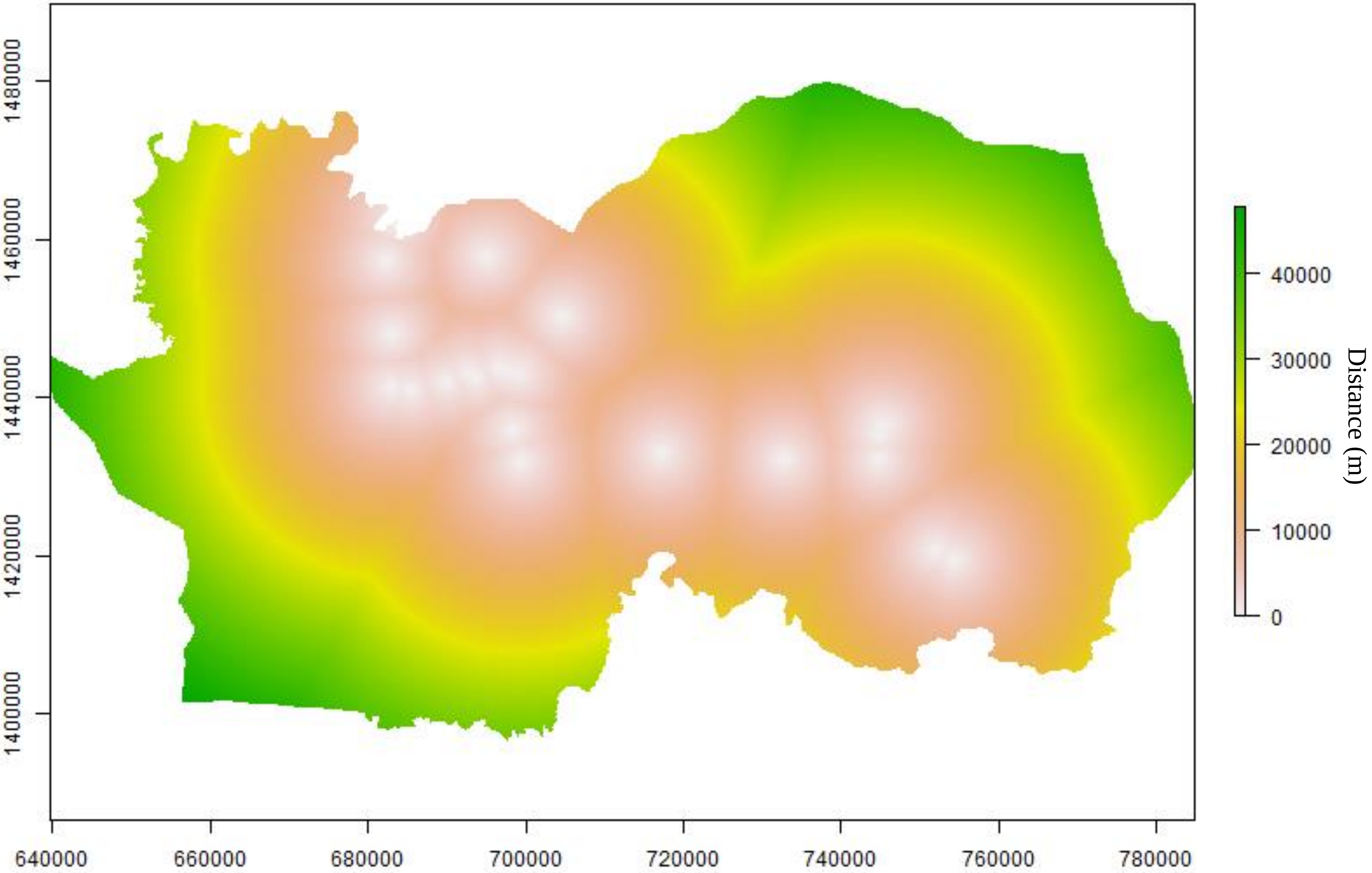


Figure 22: DistMar raster

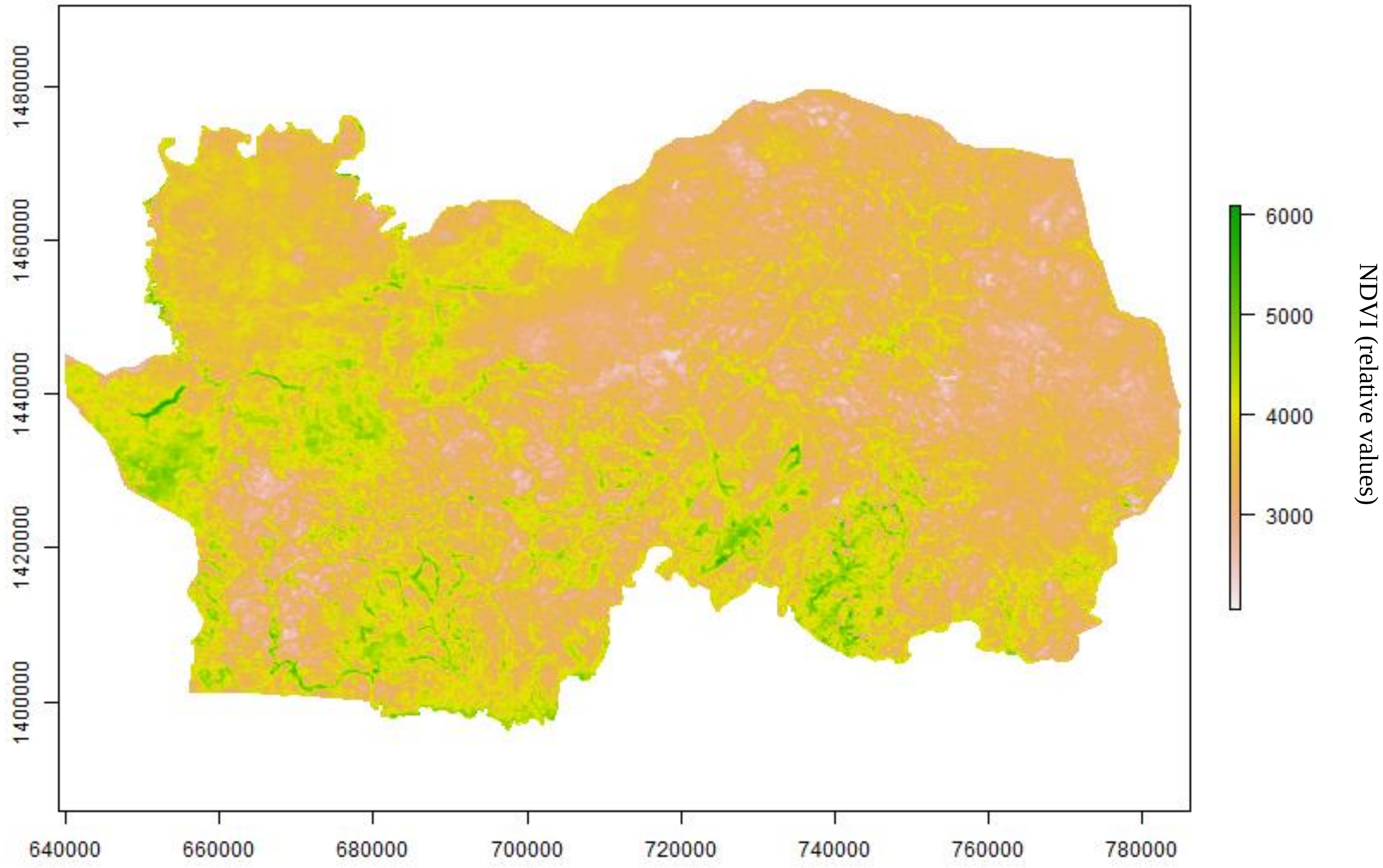


Figure 23: NDVI raster

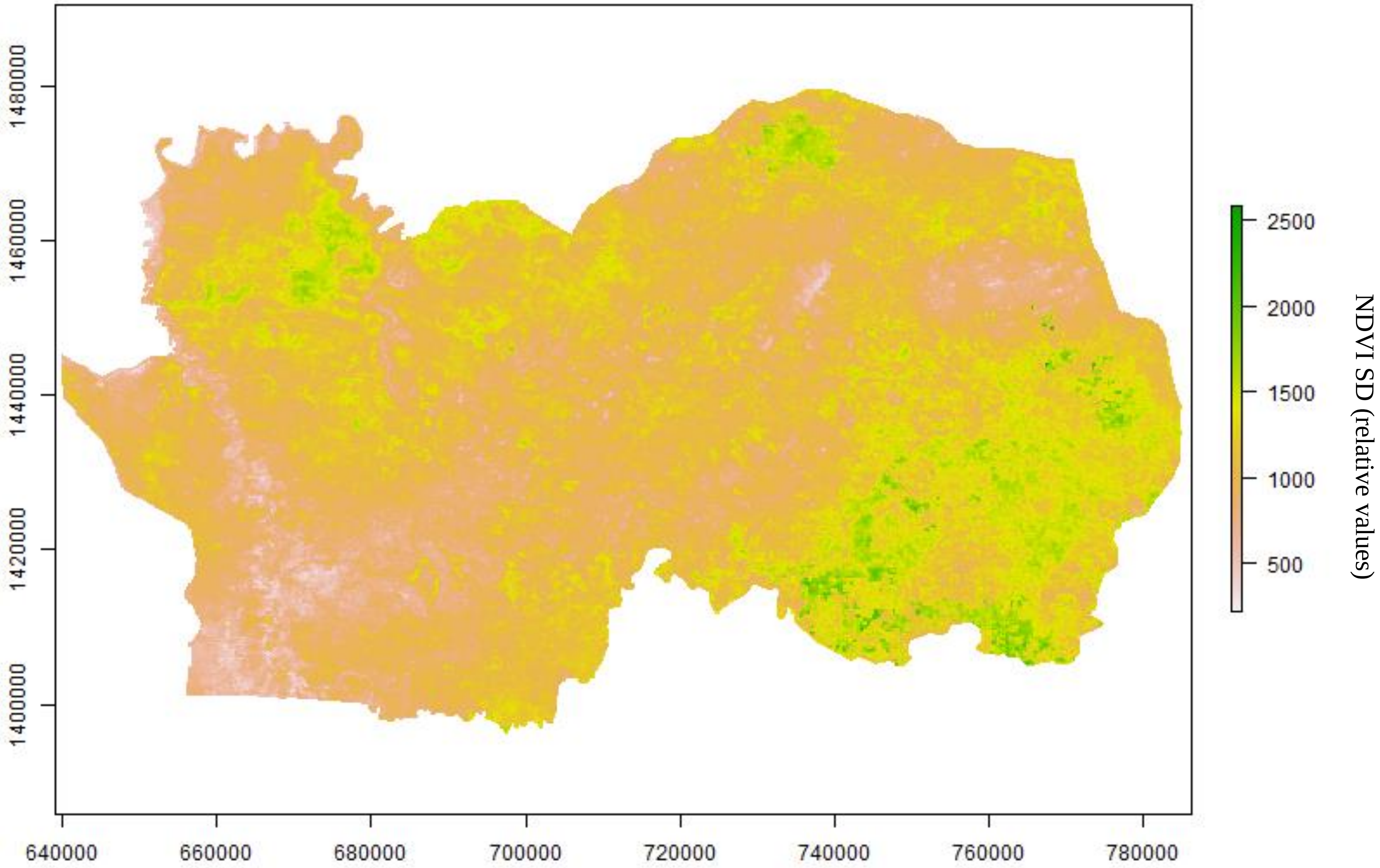


Figure 24: NDVI SD raster

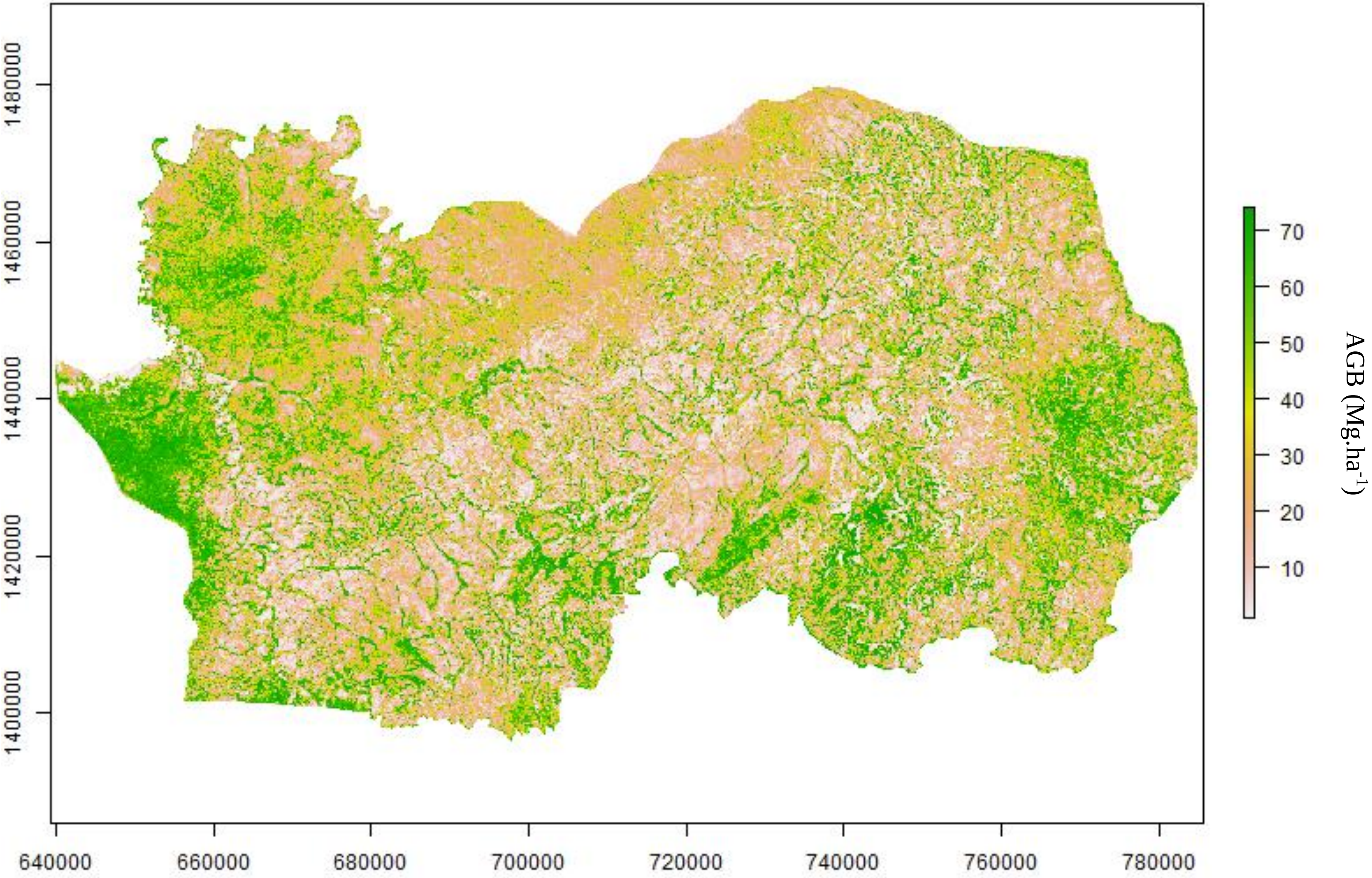


Figure 25: AGB raster

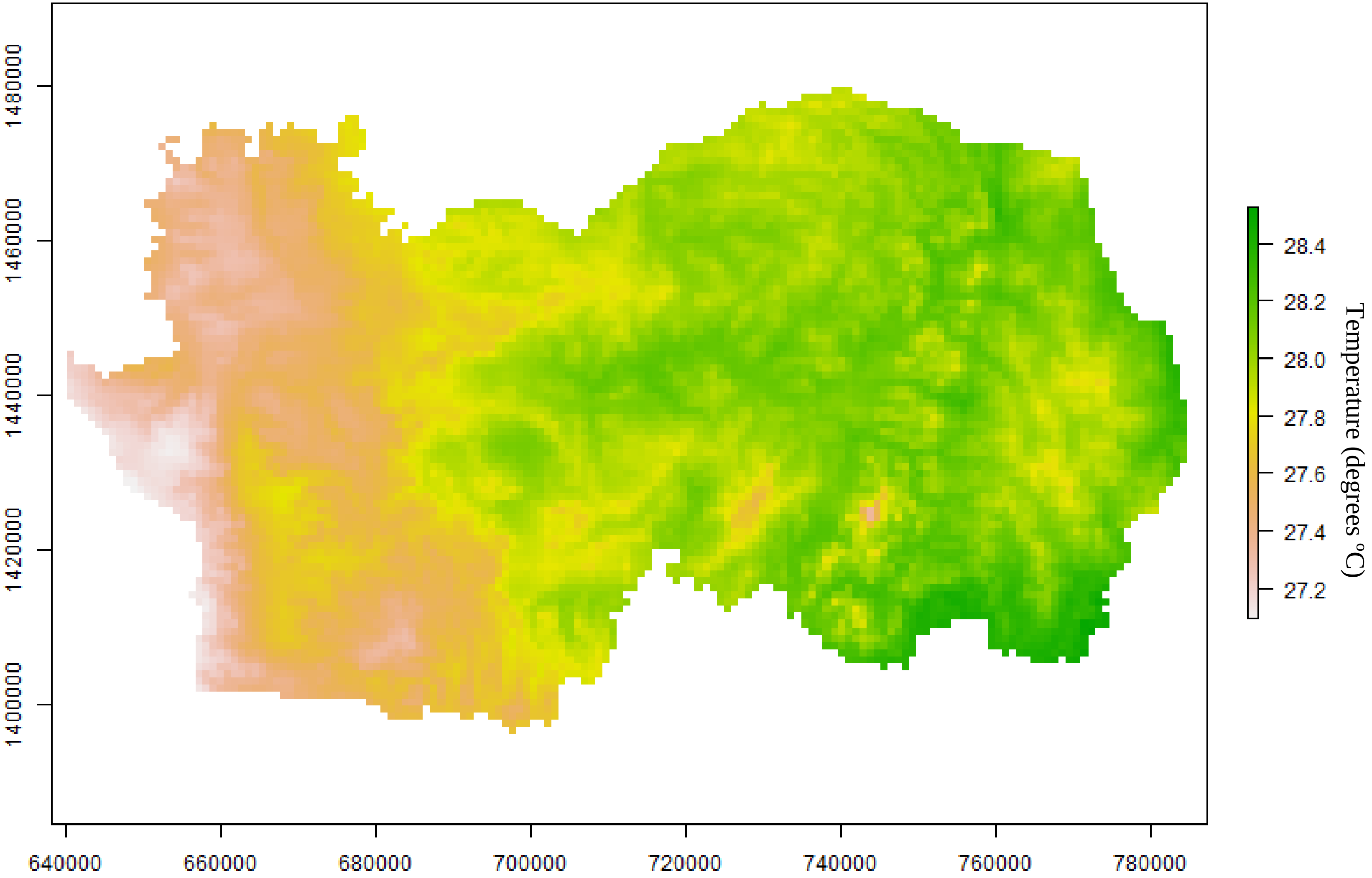


Figure 26: Bio1 raster

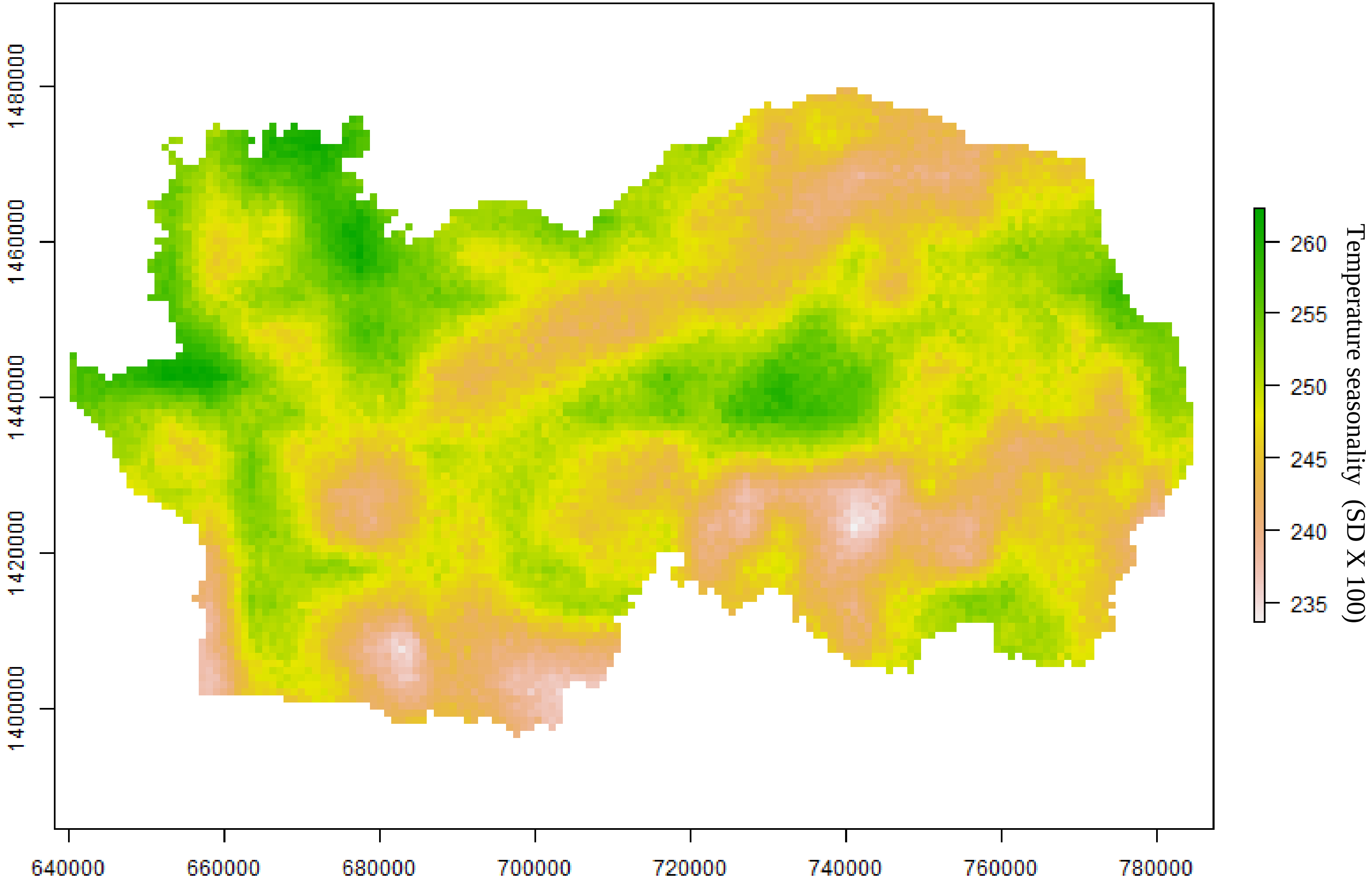


Figure 27: Bio4 raster

X

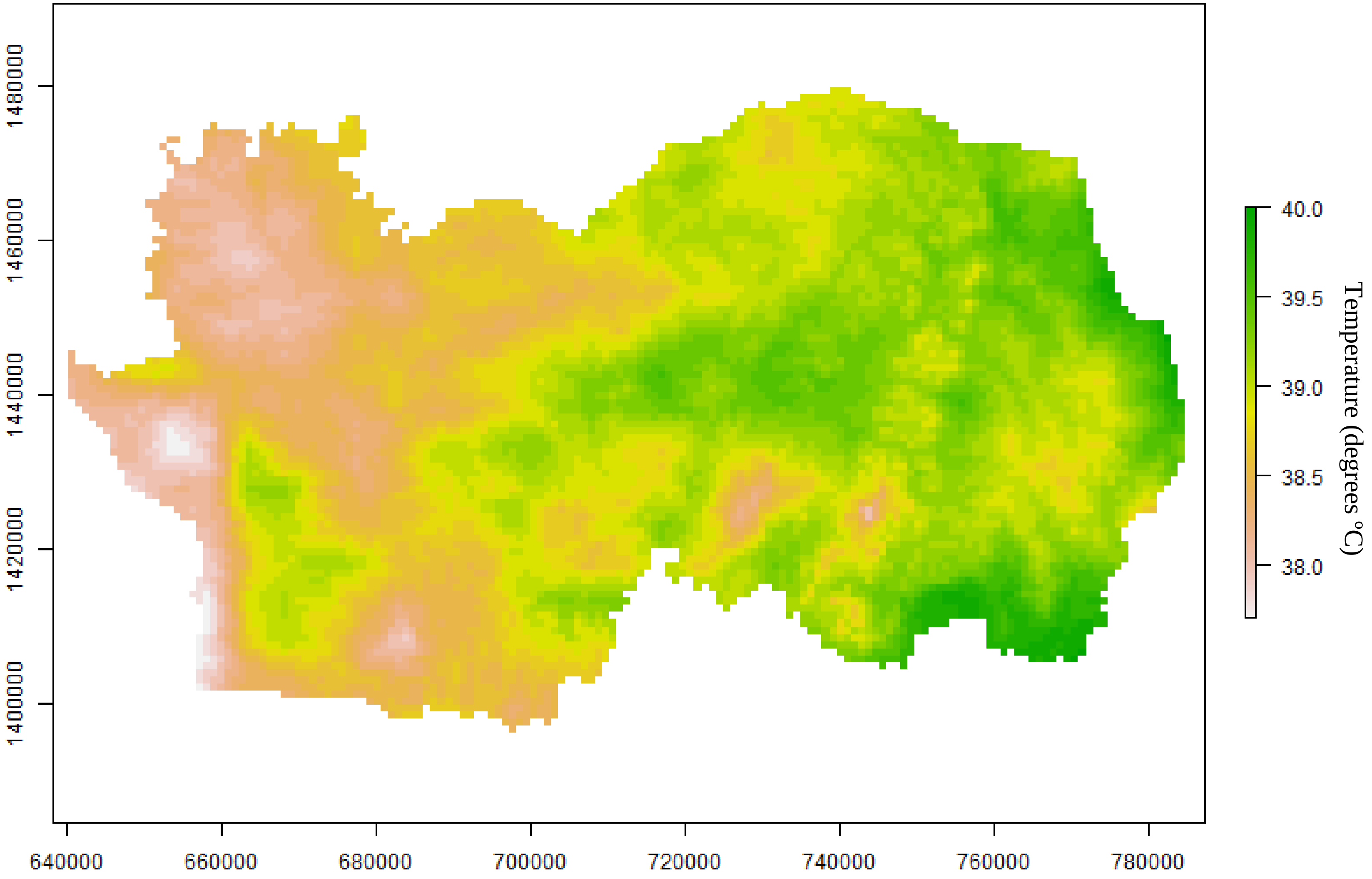


Figure 28: Bio5 raster

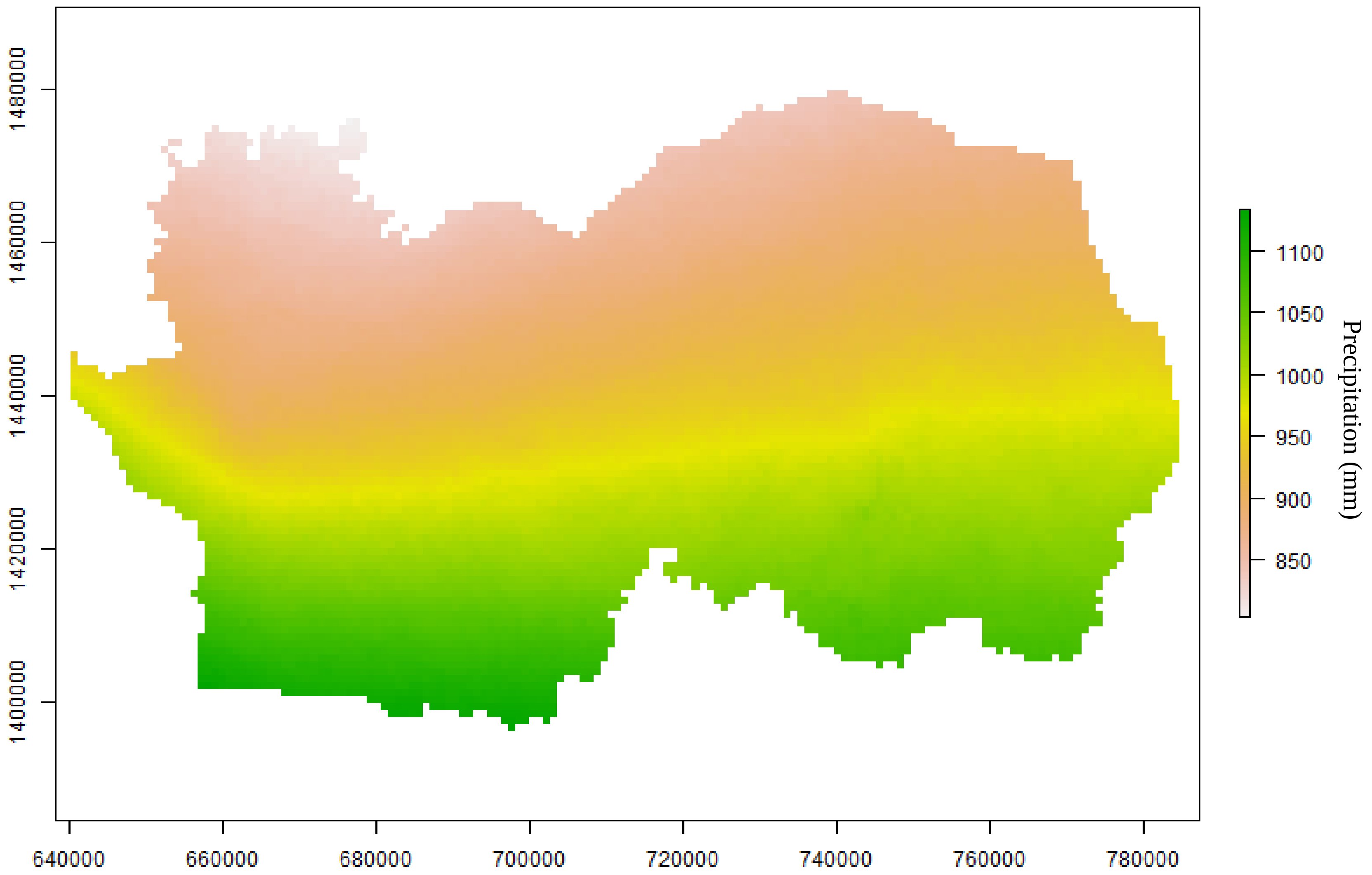


Figure 29: Bio12 raster

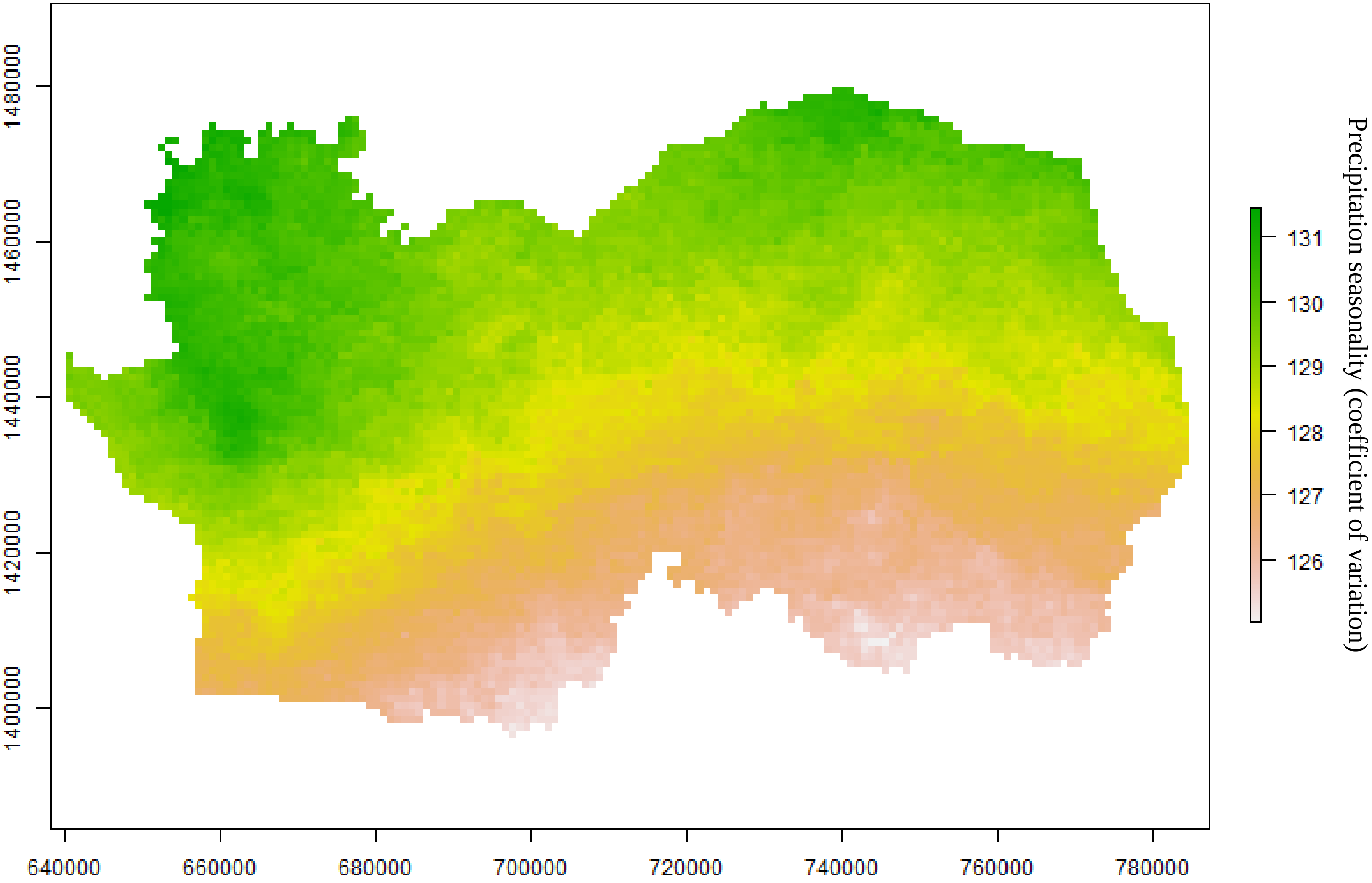


Figure 30: Bio15 raster