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Drivers of small mammals' abundance patterns in a  
South African landscape: the contexts of management  
intensity and functional groups

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## **PREFACE**

This thesis was performed in the frame of a project leaded by Prof. Lourens Swanepoel (Venda University, South Africa), aiming at assessing “Large carnivore mediated ecosystem service change”, namely targeting the importance of large carnivore populations’ in structuring ecosystems and maintaining biodiversity. Field data used in this thesis were collected by Beatriz Rosa and Gonçalo Curveira-Santos, respectively a MSc (Conservation Biology) and a PhD student (PhD Programme in Biodiversity, Genetics and Evolution) of the Faculdade de Ciências da Universidade de Lisboa, who developed their own work with the support of the above referred project.

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## RESUMO ALARGADO

A extinção de espécies no passado foi resultado de um processo natural que ocorreu sem qualquer intervenção por parte do Homem. No entanto, o aumento da taxa de extinção das espécies no Antropoceno é maioritariamente de causa humana. Uma das barreiras planetárias que a humanidade já ultrapassou foi a perda de biodiversidade (Rockstrom *et al.* 2009), devido a atividades como a desflorestação, sobrepesca e pastoreio excessivo (Vitousek *et al.* 1997; Chapin *et al.* 2000). Todas estas atividades têm impacto no habitat pois levam à alteração do uso da terra devido à degradação e conversão de habitats (Vitousek *et al.* 1997). Consequentemente, a perda de espécies conduz à redução da eficiência dos serviços e funções do ecossistema, dos quais o ser humano depende (Sala *et al.* 2000; Cardinale *et al.* 2012; Mace *et al.* 2012). Por exemplo, a redução do estrato herbáceo influencia negativamente os pequenos mamíferos, visto que estes dependem fortemente da vegetação para abrigo e comida, o que por sua vez pode reduzir a eficácia do ciclo dos nutrientes, pois os pequenos mamíferos contribuem ativamente para o ciclo do azoto através das suas fezes (Bakker *et al.* 2004, Clark *et al.* 2005).

Em África, ao longo das últimas décadas, ocorreram grandes alterações no uso do solo devido ao aumento da desflorestação e de áreas de pasto (Stephenne and Lambin 2001). A maioria das paisagens foram convertidas em quintas de gado, terras agrícolas e aglomerados urbanos, levando a uma diminuição dos ecossistemas naturais (Maitima *et al.* 2009). A descentralização das políticas públicas de conservação em África do Sul, garantiu aos donos das terras direitos sobre a vida selvagem (Pitman *et al.* 2016) o que levou à conversão dos antigos usos da terra em atividades relacionadas com a vida selvagem, tais como ranchos de animais de caça e reservas privadas para ecoturismo. Cada um destes tipos de gestão tem objetivos distintos, o que induz diferentes consequências no ecossistema. Enquanto nas quintas, o principal objetivo é maximizar a produção de ungulados para carne, nas reservas privadas o foco é a conservação do património natural, com o objetivo de maximizar o lucro da exploração, através da atração de caçadores e turistas. A presença destes e as suas atividades custeiam os gastos de manutenção de um habitat o mais natural possível e fomentam a presença de animais carismáticos e altamente valorizados economicamente como os denominados “*Big 5*” – Elefante, Rinoceronte (Preto e Branco), Búfalo, Leão e Leopardo. Coexistindo com estes dois tipos de gestão da paisagem, podemos encontrar na África austral zonas rurais, que incluem não só os aglomerados urbanos mas também áreas dedicadas à agricultura e pecuária e, por isso, possuem a maior densidade de população humana e abundância de gado doméstico comparativamente aos restantes usos do solo (Parsons *et al.* 1997).

Os pequenos mamíferos são fundamentais para o bom funcionamento do ecossistema pois contribuem para diversos serviços ecossistémicos (Avenant and Cavallini 2007). O facto de serem consumidores primários (Avenant and Cavallini 2007) faz com que sejam elos vitais na estruturação da cadeia trófica (Cameron and Scheel 2001), visto que consomem material vegetal e, paralelamente, dão suporte a uma grande comunidade de predadores, desde aves a mamíferos (Anderson and Erlinge 1977). O curto tempo geracional que os caracteriza faz com que reajam rapidamente às alterações no meio ambiente, o que os torna bons indicadores do funcionamento do ecossistema (Avenant and Cavallini 2007). Devido à diversidade e variabilidade ecológica dos pequenos mamíferos, diversos fatores já foram identificados como importantes e modeladores da estrutura populacional deste taxa, os quais podem ser, maioritariamente, determinados pelas opções de gestão (Blaum *et al.* 2006). Apesar de muitos estudos terem investigado os padrões espaciais de populações de pequenos mamíferos, poucos investigaram a comunidade de roedores de África do Sul, e existe uma lacuna de conhecimento referente ao efeito de diferentes opções de gestão na variação espacial dos padrões de abundância das espécies ou diferentes grupos funcionais.

Com o objetivo de obter esta informação, o presente estudo teve como objetivos: 1) determinar os padrões de abundância da comunidade de pequenos mamíferos residentes em KwaZulu-Natal (África do Sul); 2) determinar os fatores ambientais que mais afetam os padrões de ocupação e abundância,

através de uma abordagem funcional baseada em dois grupos de roedores (grandes e pequenos); 3) identificar quais os fatores ambientais que melhor explicam a abundância relativa de roedores a nível local/regional, de forma a prever os padrões de abundância à escala da paisagem; e 4) avaliar a influência do tipo de gestão da paisagem nos padrões encontrados de forma a compreender as consequências (ecológicas e relacionadas com a conservação) de uma gestão heterogênea da paisagem no grupo em estudo. Previu-se inicialmente que: a abundância de roedores seria mais elevada em zonas onde o estrato herbáceo é mais alto (H1), visto que confere proteção contra predadores (Bond *et al.* 1980; Delcros *et al.* 2015); a heterogeneidade do habitat terá uma influência positiva na abundância de roedores (H2), assumindo que os roedores maiores são mais influenciados, porque exploram a paisagem a uma escala maior (Sutherland *et al.* 2000, Peles and Barrett); as opções de gestão influenciam os padrões detetados, nomeadamente áreas cuja gestão permite a existência de um maior número de ungulados (Quintas e Comunidades Rurais) irão suportar comunidades de roedores menos abundantes e estes estarão mais heterogeneamente distribuídos (H3), visto que grandes abundâncias de ungulados tendem a decrescer a cobertura do solo por herbáceas e fragmentar as unidades de paisagem devido à pressão de pastoreio (Hoffman and Zeller 2005; Rautenbach 2013). No entanto, se a manutenção de pastos for uma medida de gestão das Quintas, os pequenos mamíferos podem beneficiar dessa característica apesar da competição com ungulados (Blaum *et al.* 2006) (H4).

Este estudo foi implementado na região de Maputaland em KwaZulu-Natal, África do Sul, mais concretamente em Phinda Private Game Reserve e nas áreas circundantes compostas por um mosaico de paisagens dominadas pelo homem, tal como quintas de gado selvagem, doméstico e terras Zulus. Os roedores foram amostrados com recurso a *ink tracking tunnels* que permitem aos indivíduos marcarem as suas pegadas para posterior identificação. Foram utilizadas *boosted regression trees* (Elith *et al.* 2008) que permitiram analisar a influência nas variáveis ambientais na abundância de roedores, tal como avaliar o comportamento da abundância em função das mesmas. Com base nestes resultados, foi elaborado um mapa preditivo da distribuição dos roedores para as três áreas de estudo.

Os resultados demonstraram que os fatores que mais influenciam os padrões de distribuição dos roedores são mais determinados pelos grupos funcionais em estudo (grandes e pequenos roedores) do que pela área em si. No que toca às previsões, confirma-se a importância da vegetação para os pequenos mamíferos (H1) bem como a influência negativa da presença de ungulados (H3). Apenas não foi possível corroborar a importância da heterogeneidade do habitat para os grupos em estudo (H2). Foi possível verificar, através da análise da abundância, que Phinda é o habitat mais adequado para os pequenos mamíferos, seguido pelas quintas. As zonas rurais, estando visivelmente mais degradadas, suportam a menor abundância de roedores. É importante reconhecer as quintas e as reservas como locais importantes para a conservação de pequenos mamíferos, pois ambas suportam abundâncias elevadas de roedores. Os padrões de distribuição diferem, provavelmente por existir competição ou partição do nicho entre os dois grupos funcionais, sendo os grandes roedores o grupo dominante. No geral, o presente estudo demonstra que os diferentes tipos de gestão em África do Sul afetam diferencialmente a comunidade de roedores estudada, e que a divisão em grupos funcionais revela diferenças ecológicas que devem ser consideradas aquando de definição dos planos de gestão e conservação destes taxa.

**Palavras-chave:** Amostragem não-invasiva, Modelação ecológica, Opções de gestão, Conservação

## ABSTRACT

In the past, the extinction of species was the result of a natural process that occurred without any intervention by Man. However, the increase in extinction rate of species in the Anthropocene is mostly of human cause. One of the planetary boundaries that humanity has already exceeded is biodiversity loss (Rockstrom *et al.* 2009) due to activities such as deforestation, overfishing and overgrazing (Vitousek *et al.* 1997; Chapin *et al.* 2000). All these activities have an impact on habitat as they lead to land use change, due to habitat degradation and conversion (Vitousek *et al.* 1997). Consequently, species loss leads to the reduction of ecosystem services and functions efficiency on which humans depend (Sala *et al.* 2000; Cardinale *et al.* 2012; Mace *et al.* 2012). For example, reducing herbaceous stratum negatively influences small mammals as they rely heavily on vegetation for shelter and food, which in turn can reduce the effectiveness of the nutrient cycle, as small mammals actively contribute to the nitrogen cycle through their faeces (Bakker *et al.* 2004, Clark *et al.* 2005).

In Africa, over recent decades, major changes in land use have occurred due to increase in deforestation and grazing areas (Stephennie and Lambin 2001). Most landscapes have been converted to cattle ranches, farmland and urban settlements, leading to a decline in natural ecosystems (Maitima *et al.* 2009). The decentralization of public conservation policies in South Africa gave landowners rights over wildlife (Pitman *et al.* 2016) which led to the conversion of former land uses into wildlife-related activities such as game ranches and private reserves for ecotourism. Each of these types of management has different objectives, which induce different consequences on the ecosystem. While in farms, the main objective is to maximize the production of ungulates meat, in private reserves the focus is on the conservation of the natural heritage, with the aim of maximizing the profitability of exploration through the attraction of hunters and tourists whose presence and activities support the cost of maintaining a habitat as natural as possible, foster the presence of charismatic and highly valued animals such as the so-called “Big 5” - Elephant, Rhino (Black and White), Buffalo, Lion and Leopard. Coexisting with these two types of landscape management, rural areas can be found in southern Africa, which include not only urban settlements but also areas devoted to agriculture and livestock, thus having the highest human population density and abundance of domestic livestock, compared to other land uses (Parsons *et al.* 1997).

Small mammals are critical to the proper functioning of the ecosystem as they contribute to various ecosystem services (Avenant and Cavallini 2007). Being primary consumers (Avenant and Cavallini 2007) makes them vital links in structuring the food chain (Cameron and Scheel 2001) as they consume plant material and in parallel support a large community of predators, from birds to mammals (Anderson and Erlinge 1977). The short generational time that characterizes them, makes them react quickly to changes in the environment, which makes them good indicators of ecosystem functioning (Avenant and Cavallini 2007). Due to the diversity and ecological variability of small mammals, several factors have already been identified as important and modellers of population structure of this taxa, which can be largely determined by management options (Blaum *et al.* 2006). Although many studies have investigated the spatial patterns of small mammal populations, few have investigated the South African rodents' community, and there is a knowledge gap regarding the effect of different management options on spatial variation in species abundance patterns or different functional groups.

In order to obtain this information, the present study aimed to: 1) determine the abundance patterns of small mammals' community living in Kwazulu-Natal region; 2) determine the main environmental factors affecting observed occupancy and abundance patterns, and how these vary between areas with distinct management goals and between functional groups (big and small rodents); 3) use the variability of the environmental factors that best explain the local/regional relative abundance of rodents groups to predict the abundance patterns at the landscape scale; 4) evaluate the influence of landscape management options on the detected abundance patterns and drivers of importance in order to understand the consequences (ecological and conservation-wise) of heterogeneous management over the focal taxa. It

was initially predicted that: rodent abundance would be higher in areas where the herbaceous stratum is taller (H1), as it provides protection against predators (Bond *et al.* 1980; Delcros *et al.* 2015); habitat heterogeneity will have a positive influence on rodent abundance (H2), assuming that larger rodents are more influenced because they explore the landscape on a larger scale (Sutherland *et al.* 2000, Peles and Barrett 1996); management options influence the detected patterns, namely areas whose management allows a larger number of ungulates (Farms and Rural Communities) will support less abundant rodent communities and these will be more heterogeneously distributed (H3), as large abundances of ungulates tend to decrease herbaceous land cover and fragment landscape units due to grazing pressure (Hoffman and Zeller 2005) ; Rautenbach 2013) However, if grazing is a farm management measure, small mammals may benefit from this feature despite competition with ungulates (Blaum *et al.* 2006) (H4). This study was carried out in the Maputaland region of KwaZulu-Natal, South Africa, more specifically in Phinda Private Game Reserve and the surrounding areas made up of a mosaic of human-dominated landscapes such as farms with wild and domestic ungulates and Zulus lands. Rodents were sampled using ink tracking tunnels that allow individuals to mark their tracks for later identification. Boosted regression trees (Elith *et al.* 2008) were used to analyse the influence of environmental variables on rodent abundance, as well as to evaluate abundance behaviour in relation to them. Based on these results, a predictive map of rodent distribution for the three study areas was prepared. The results showed that the factors that most influence rodent distribution patterns are more determined by the functional groups under study (big and small rodents) than by the area itself. As for my predictions, the importance of vegetation for small mammals (H1) as well as the negative influence of the presence of ungulates (H3) is confirmed. It was not possible to corroborate the importance of habitat heterogeneity for the study groups (H2). Through abundance analysis it was possible to verify that Phinda is the most suitable habitat for small mammals, followed by Farms. Rural Communities, being noticeably more degraded, bear the least abundance of rodents. It is important to recognize farms and reserves as important places for the conservation of small mammals, as both bear high rodent abundances. Distribution patterns differ, probably because there is competition or niche partitioning between the two functional groups, with big rodents being the dominant group. Overall, the present study demonstrates that the different types of management in South Africa differentially affect the rodent community studied, and that the division into functional groups reveals ecological differences that should be considered when defining management and conservation plans for these taxa.

**Keywords:** Non-invasive sampling, Ecological modelling, Management options, Conservation

## INDEX

<b>AGRADECIMENTOS</b> .....	<b>iii</b>
<b>RESUMO ALARGADO</b> .....	<b>iv</b>
<b>ABSTRACT</b> .....	<b>vi</b>
<b>GENERAL INTRODUCTION</b> .....	<b>x</b>
<b>Article</b> .....	<b>1</b>
<b>1. Abstract</b> .....	<b>1</b>
<b>2. Introduction</b> .....	<b>2</b>
<b>3. Materials and methods</b> .....	<b>4</b>
3.1. Study area .....	4
3.2. Small mammals' sampling .....	5
3.3. Environmental variables collected during the field work.....	6
3.4. Variables collected from remote sensing products.....	8
3.5. Data analyses/modelling.....	10
<b>4. Results</b> .....	<b>11</b>
4.1. Multicollinearity between independent variables.....	11
4.2. Drivers of abundance.....	11
4.3. Spatial patterns of rodents' abundance across areas and functional groups .....	13
<b>5. Discussion</b> .....	<b>16</b>
<b>6. References</b> .....	<b>23</b>
<b>GENERAL CONCLUSION</b> .....	<b>xii</b>
<b>REFERENCES</b> .....	<b>xiii</b>
<b>APPENDIX</b> .....	<b>xv</b>



## LIST OF FIGURES

Figure 3.1- Map of the study area: a) Map of South Africa, b) representing the three types of lands with distinct management schemes and c) scheme with sampling point arrangement .....	4
Figure 3.2- Ink tracking tunnel scheme .....	5
Figure 4.1- Function fitted for the most important predictors by a boosted regression tree (BRT) relating the abundance of small rodents to each environmental variable.....	12
Figure 4.2- Function fitted for the most important predictors by a boosted regression tree (BRT) relating the abundance of big rodents to each environmental variable. ....	13
Figure 4.3- Boxplot of rodents' relative abundance in the three management types zones monitored: Farms, Phinda reserve and Rural Communities. ....	13
Figure 4.4- Map of the study area showing both rodents' distributions .....	14
Figure 4.5- Map of the study area showing the predicted distribution of both rodent' groups. ...	15
Figure 4.6- Boxplot representing mean and SD values for functional groups per area, comparing values from prediction and original abundance values (raw).....	16

## LIST OF TABLES

Table 3.1- Environmental variables collected during the field work and used as candidate variables in the modelling procedure .....	6-7
Table 3.2- Environmental variables collected during the field work, using camera-trapping, and used as candidate variables in the modelling procedure.....	7
Table 3.3- Categories used to describe the abundance of wild ungulates detected during the camera-trapping campaigns .....	8
Table 3.4- Environmental variables from geographic information systems (GIS) used as candidate variables in the modelling procedure . ....	9
Table 4.1- Results of Lloyd's Index of Patchiness .....	14

## GENERAL INTRODUCTION

Species extinction has always occurred even without any human intervention. However, the increase in extinction rate in Anthropocene is mostly of human cause. Biodiversity loss is one of the planetary boundaries that humankind already exceeded (Rockstrom *et al.* 2009). A study focusing on birds showed that conversion of natural habitats into cropland and pasture is responsible for 37% of threats to globally threatened bird species (BirdLife International 2000; Green *et al.* 2005). Furthermore, according to IUCN Red List, 25% of mammal species are threatened with extinction in 2019 (IUCN Red List 2019). The main drivers of these declines are related with human activities, from air and water pollution, to deforestation and overgrazing (Vitousek *et al.* 1997; Chapin *et al.* 2000). All these activities induce a land use change, which is considered the major driver of biodiversity loss, affecting over 2,000 mammals (Vitousek *et al.* 1997, MEA 2005). Habitat loss is the greatest threat to wildlife globally, causing population shrinkage and consequentially, increasing the probability of extinction by stochastic events (Burkey 1995). When habitat conditions get deteriorated, animals are forced to move to adjacent habitats that meet the necessary conditions for their survival (Tilman *et al.* 2017). If, to survive, preys are forced to move to new sites, predators will follow its food supply, since prey have the ability of changing predators' population cycles (Yoshida *et al.* 2003). Thus, changes affecting prey can have cascading implications for the entire food chain. Therefore, species loss threatens to collapse ecosystems across the world.

Most changes in terrestrial ecosystems are associated with resource extraction to meet human needs due to high population growth. Conversion of natural habitats into pasture land, farmland and urban areas is one of the most common changes that have occurred in several ecosystems (Vitousek 1997). Significant land use changes have occurred in Africa in the past few decades, being the most striking alterations caused by deforestation and overgrazing (Stephene and Lambin 2001). Savannas ecosystems were mainly affected when Europeans introduced domestic cattle and sheep, causing the reduction and elimination of indigenous large mammals and their predators (Walker 1981). These modifications lead to changes in vegetation, increasing woody and thicket areas instead of original grass species (Walker 1981), leading to dramatic alteration in the floristic composition of savannas.

Conservation emerged in context of the extinction crisis due to habitat loss (Noss 1999). Rapidly it focused on habitat protection and landscape-level processes, to counteract the previous impacts (Goldman 2009). The focus of landscape-level efforts has enabled conservation not only to be applied at national parks and community zones, but at a much broader scale (Goldman 2009). These measures emerged to improve habitat management in order to allow land use in harmony with native species. Conservation in South Africa is settled on several agencies, from national to provincial levels, whose function is to develop management strategies and apply them to their natural resources (King 2009). However, the decentralization of the public conservation policies granted wildlife rights to individual landowners (Pitman *et al.* 2016) that caused the conversion of agricultural farms and cattle ranches into wildlife-related activities such as game ranches and private reserves for ecotourism. This measure had a considerable positive effect on wildlife as it led to the renaturalization of most of the former pastoral and farmland systems, allowing to accommodate a greater number of native species, especially those attractive for tourism (ex. Big 5 – Elephant, Rhino (Black and White), Buffalo, Lion e Leopard), but contributed even more for the land use change. These trends resulted in complex landscapes, especially where contrasting management scenarios coexist in relatively small scales.

In this context, one of the questions that needs to be addressed is the impact of these habitat changes on native species, especially those with great contribution for the proper functioning of the ecosystem. Small mammals are a group that fits the description above, as they contribute to several activities that are critical in the ecosystem. They contribute to the loosening and aeration of the soil through tunnels and burrows (Jones *et al.* 1994), and even in low densities, they are important sources of food for many

predators, from other mammals to reptiles and birds of prey (Andersson and Erlinge 1977; Hayward and Phillipson 1979; Salamolard *et al.* 2000, Jonsson *et al.* 2000). Thus, small mammals play an important role in the trophic chain in most of the world ecosystems. African meso-carnivores (e.g. large-spotted genet) are no exception and their diet is largely composed by small mammals, these being consequently a crucial driver of habitat selection by these predators (Thompson and Gese 2007). Therefore, to fully understand mesocarnivores spatial ecology, which is essential to plan their management and to understand their ecology (Marker *et al.* 2008), is mandatory to assess small mammal's richness and abundance patterns across space.

Several rodents are omnivorous, being, consequently, a very important energy and nutrient vehicle between many primary producers and secondary consumers (Hayward and Phillipson 1979). Their role in the nutrient cycle is also well-known. Since their faeces are widely distributed and small, they decompose rapidly, providing nitrogen on a fast and efficient way to plants (Bakker *et al.* 2004; Clark *et al.* 2005). Small mammals are also considered bioindicators of habitat integrity because they react rapidly to changes in the environment due to their short generation time, high breeding rate, and dependence of microhabitat conditions to survive (Cameron and Scheel 2001; Avenant and Cavallini 2007). Due to all these reasons, they are directly influenced by local environmental variables, which makes them adequate biological models particularly useful for conservation strategies, with implications to the entire trophic chain.

Small mammals are extremely affected by land use changes, since these are responsible for modifications in the environment, especially in vegetation (Sala *et al.* 2000; Cameron and Scheel 2001, Avenant and Cavallini 2007). Since small mammals' abundance is mainly determined by vegetation characteristics, changes in the environment can lead to severe variations in their abundance (Avenant and Cavallini 2007). Vegetation removal for agriculture and farming reduces shelter and food availability for small mammals, what have negative implications in their survival (Keesing 1998; Hoffman and Zeller 2005). Therefore, is important to access how different management strategies affect small mammals and define conservation measures in order to avoid conflict between land use and small mammals' distribution.

# **Drivers of small mammals' abundance patterns in a South African landscape: the contexts of management intensity and functional groups.**

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## **1. Abstract**

South African laws that attributed custodial rights to landowners over wildlife, led to a decentralization of conservation, from state to private reserves. This responsibility changes, together with the distinct management option implemented by reserves, created a mosaic of different land uses, increasing the complexity of wildlife management and conservation regimes rooted in heavily human-dominated landscapes. All these landscape modifications have impacts on local biodiversity, which can have future implications on ecosystem's functioning. The present study aims to determine the effect of different environmental factors (including management schemes) on the southern African small mammal community occurrence patterns, by comparing protected/native habitats with those altered by human activities, through a functional approach, using two rodents' groups (big and small) as models. Furthermore, I tested if a given environmental driver can be used as an environmental indicator to detect the effect of land use changes in small mammals' communities. Rodents were sampled between October and November 2017 using ink tracking tunnels, in Phinda Private Game Reserve (South Africa) and in the surrounding game farms and human settlements of the Zulu tribal authority land. A boosted regression trees approach was used to test the influence of environmental variables on rodents' relative abundance. My results show that the most influential drivers of rodents' abundance were ungulates presence, influencing negatively, followed by vegetation metrics (ex. Shrub Height, positively). Overall, sites that host greater rodents' abundances are those that are less disturbed by human activities, but have essential conditions for the survival of rodents, by providing food and shelter. There are differences in rodents' abundance patterns between land uses and between functional groups, indicating distinct ecological requirements of each group and different influences of each type of management. Overall, this study supports the idea that different functional groups are influenced in distinct ways by land use practices.

**Keywords:** Non-invasive sampling, Ecological modelling, Management options, Conservation

## 2. Introduction

Biodiversity loss is one of the planetary boundaries that humankind already exceeded (Rockstrom *et al.* 2009). Human activities are the root cause of this problem due, for example, to deforestation, overfishing and overgrazing (Vitousek *et al.* 1997; Chapin *et al.* 2000). All these activities will induce a land use change, which is considered the major driver of biodiversity loss (Vitousek *et al.* 1997, MEA 2005). As a result of natural habitats' conversion, species are being extinguished by loss of essential resources, which leads to a decrease in ecosystem functions and services (Sala *et al.* 2000; Cardinale *et al.* 2012; Mace *et al.* 2012).

Significant land use changes occurred in Africa in the past few decades, being the most striking alterations caused by deforestation and overgrazing (Stephene and Lambin 2001). Most landscapes were converted into cattle ranches and farmlands, leading to the destruction, degradation and/or fragmentation of natural ecosystems (Maitima *et al.* 2009). In South Africa, the government passed laws attributing custodial rights over wildlife to landowners, which promoted decentralization of the conservation efforts from the state to privates (Pitman *et al.* 2016). This measure caused the conversion of the previous land uses, i.e. farmlands and cattle ranches, into others targeting activities related with wildlife, such as game ranching and private game/ecotourism reserves. Each of these land management systems have quite contrasting underlying objectives with consequences on the landscape structure and wildlife ecological patterns. While in game farms the main objective is to maximize the production of ungulates for meat and the creation of grasslands is a requisite in order to increase grazing area, in private game reserves the naturalization of the prevailing habitat is required, since the goal is to focus on charismatic species conservation, that will serve as umbrella for the conservation of the remaining species. Side to side, communal lands support the highest density of humans and have a similar stocking rate than the other areas, despite including more domestic cattle (Parsons *et al.* 1997). The regional co-existence of all these management systems thus generate a human-dominated disturbance/landscape gradient. For example, a study located at 30km north-west of Kimberley, South Africa, showed a higher density of trees, shrubs and bare soil (and lower herbaceous cover) in communal lands, which appear to be the most degraded system due to overgrazing (Smet and Ward 2005). Private game reserves, on the other hand, have the most attractive conditions for wildlife, representing a land cover more like natural ecosystems (Parsons *et al.* 1997). Game farms present an intermediate situation where ungulates are maintained within a rotational system, avoiding overgrazing (Parsons *et al.* 1997).

Furthermore, humans' attitudes towards wildlife, namely carnivores, differ between land use type, which can have a cascading effect upon the lower trophic level species and, consequently, on the vegetation structure (Lindsey *et al.* 2005). While in private game reserves big predators are valuable for tourism, in farms they are often killed (Lindsey *et al.* 2005). Therefore, predators' abundances vary according to the land use type. Small carnivores, on the other hand, are less reported as conflict cause (Romañach *et al.* 2007, Blaum *et al.* 2009). However, they directly compete with domestic animals, such as cats and dogs, in what concerns to food. Most small carnivores include rodents in their diet (Mukherjee *et al.* 2004), and cats and dogs can also prey on small mammals leading to direct competition. In the absence of predators, rodents' abundance can increase greatly, and even become a plague, which has negative consequences on the ecosystem, acting as disease vectors (ex. Hantavirus) or crop destruction agents (Fiedler 1988; Williams *et al.* 2018, Guterres and Lemos 2018). Thus, the consequences of the management type and human attitudes towards wildlife have a great influence on the biodiversity values of each landscape component. For instance, when grazing pressure is too high, there is an increase in humidity and space availability that allow the establishment of shrubs and, consequentially, its encroachment (Caldwell *et al.* 1978). This will lead to a decrease in available resources for species that feed mainly on grasses, such as small mammals (Iwala *et al.* 1979).

Due to their high diversity and variation in ecological requirements, several factors have been identified as influential in shaping rodents' community and population structure, and these can be mainly determined by the landscape management options. Studies focused on rodents around the world have pointed out vegetation type and traits as fundamental drivers of the occurrence and abundance patterns of these small mammals (Williams *et al.* 2002; Layme *et al.* 2004; Holland and Bennett 2009). Namely, areas with greater herbaceous coverage favour small mammals by providing shelter against predators, food and adequate microclimatic conditions, for example by retaining moisture at the ground level (Hoffman and Zeller 2005). In addition, a higher herbaceous height supports a larger number of species and higher populational abundances (Monadjem 1997), and studies have shown negative effects of overgrazing in small rodents, by reducing the herbaceous stratum, increasing trampling risk and feeding competition with ungulates (Keasing 1998; Hoffman and Zeller 2005; Rautenbach 2013). Furthermore, landscape's complexity seems to influence positively small mammals, because it increases microhabitats diversity and availability of different niches (Fischer *et al.* 2011). In Africa, soil cover, whether it be grasses, shrubs or rocks, also proved its positive importance for the various species of small mammals (Bond *et al.* 1980; Delcros *et al.* 2017). Another important factor is elevation, which is the most correlated variable with *Mastomys natalensis*' distributional pattern, a common rodent' species in South Africa, indicating its preference for low altitudes (Venturi *et al.* 2004). On smaller scales, differences in altitude can be associated with microhabitat diversity, which is an important requisite for small mammals (Fischer *et al.* 2011).

Understanding the most influential impacts on small mammals' patterns, and the acting ecological mechanism is particularly important, because this taxon is a fundamental piece for the proper functioning of the ecosystem puzzle (Avenant and Cavallini 2007). The fact that they are primary consumers (Avenant and Cavallini 2007) and support a large community of predators (Andersson and Erlinge 1977, Jonsson *et al.* 2000) makes them vital links in food chains structuring (Cameron and Scheel 2001). They contribute strongly to the nitrogen cycle (Bakker *et al.* 2004, Clark *et al.* 2005) and react rapidly to changes in habitat, undergoing fluctuations in diversity and density. Small mammals are thus considered to be useful tools for describing and monitoring habitat integrity and, therefore, considered good indicators of ecosystem functioning (Avenant and Cavallini 2007).

Although several worldwide studies have investigated the spatial patterns of small mammals (Canova 1992; Simone 2010; Wolf 2015), few studies have explored the effect of different environmental factors on the South African rodents' community, by comparing protected/native habitats characteristics altered habitats due to cattle raising and other human activities (Blaum *et al.* 2006; Gardner *et al.* 2007; Caro 2011 ); nor tested the usefulness of a given environmental driver as an ecological indicator to detect the effect of land use changes in small mammals' communities and forecast population variations associated with such factor alterations. Since there is a lack of information regarding the drivers of small mammals' abundance patterns in a South African landscape, as well the patterns of change associated with the landscape management intensity and the functional groups considered, this study has four main objectives: 1) determine the abundance patterns of small mammals' community living in Kwazulu-Natal region; 2) determine the main environmental factors affecting observed occupancy and abundance patterns, and how these vary between areas with distinct management goals and between functional groups (big and small rodents); 3) use the variability of the environmental factors that best explain the local/regional relative abundance of rodents groups to predict the abundance patterns at the landscape scale; 4) evaluate the influence of landscape management options on the detected abundance patterns and drivers of importance in order to understand the consequences (ecological and conservation-wise) of heterogeneous management over the focal taxa.

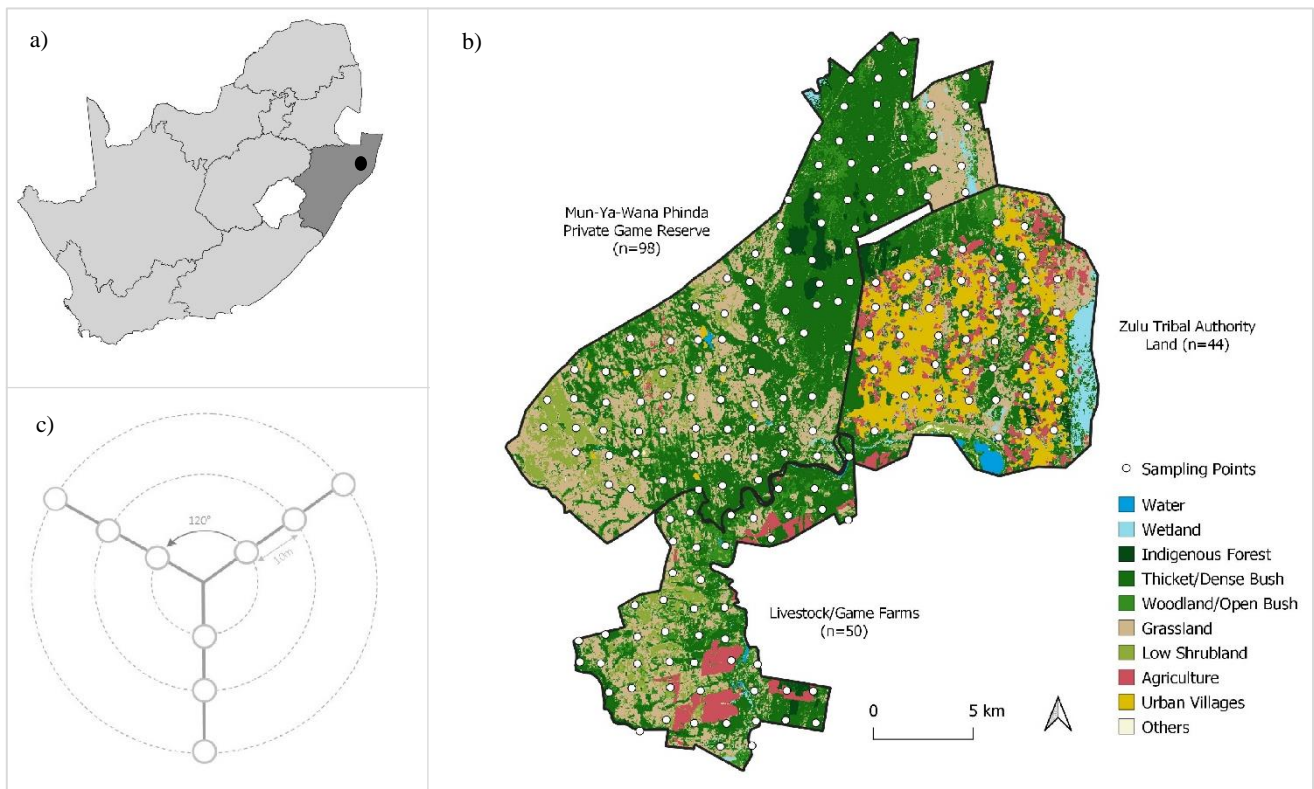
To fulfil these objectives, I formulated several hypotheses to be tested in this study: H1- the abundance of both rodents' groups is higher in places where the herbaceous stratum is taller, since such structure provides protection against potential predators (Bond *et al.* 1980; Monadjem 1997; Delcros *et*

al. 2015); H2 - habitat heterogeneity has a positive influence on the abundance of rodents, assuming that larger rodents are more influenced because they explore the landscape at larger scales (Sutherland *et al.* 2000, Peles and Barrett 1996); H3 - management options influence the detected patterns, namely areas whose management allows a larger number of ungulates (Farms and Rural Communities) will support less abundant rodent communities and these will be more heterogeneously distributed (H3), as large abundances of ungulates tend to decrease herbaceous land cover and fragment landscape units due to grazing pressure (Hoffman and Zeller 2005; Rautenbach 2013). However, if grazing is a farm management measure, small mammals may benefit from this feature despite competition with ungulates (Blaum *et al.* 2006) (H4).

### 3. Materials and methods

#### 3.1. Study area

This study was implemented in the Maputaland region of northern KwaZulu-Natal in South Africa, more specifically in the Phinda Private Game Reserve and in the surrounding game farms and human settlements of the Zulu tribal authority land (Figure 3.1c). The region is characterized by a warm temperature climate, fully humid with a hot summer (October to April), according to Köppen-Geiger classification. Mean monthly temperatures range from 31°C in January to 19°C in July, and the average annual precipitation is 500mm (South African Weather Service). Elevation ranges from 4m to 350m, allowing the existence of 11 distinct vegetation types, dominated by a mixture of bushveld (38%), woodland (13%) and grassland (5%) (Rautenbach 2013) (Figure 3.1). Phinda Private Game Reserve

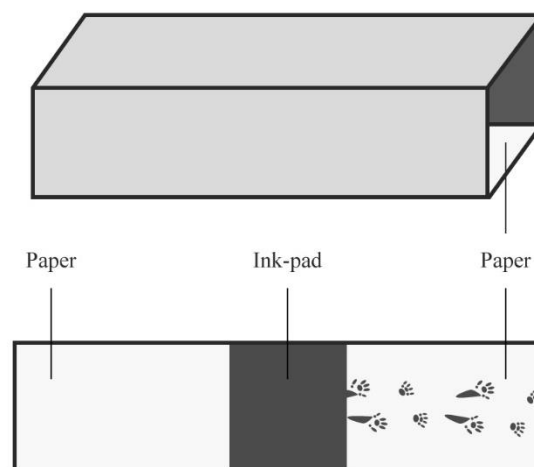


**Figure 3.1** - Map of the study area - a) Map of South Africa with the black point representing the location of the study area; b), representing the three areas with distinct management schemes that were studied: Phinda Game Reserve, Livestock/Game Farms and Zulu Tribal Land. c) Each point on the map represents a sampling point, consisting of a camera trap in the centre and nine ink tunnels. Each area had a different number of sampling points, indicated in the legend above. In c) are illustrated the most common land use types in the study area, listed in the figure.

(PPGR, 27° 40'S - 27° 55'S; 31° 12'E - 32° 26'E) is a 220km<sup>2</sup> game reserve situated on a flat coastal plain in the Maputaland region, one of the world's biodiversity hotspots (Balme *et al.* 2010). A wide range of species inhabits the reserve including forty-four large mammals like cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), lion (*Panthera leo*), buffalo (*Syncerus caffer*) and elephant (*Loxodonta africana*) (Balme *et al.* 2010), mesocarnivores such as white-tailed mongoose (*Ichneumia albicauda*), large-spotted genet (*Genetta tigrina*) and honey badger (*Mellivora capensis*), and about thirty rodents' species (Apps 1996; Kingdon *et al.* 2013). The game reserve is surrounded by a mosaic of human-dominated landscapes, such as game farms and Zulu tribal authority land (Figure 3.1c). Game farms are mainly composed by natural habitat and low human densities, while Zulu tribal land consists essentially of pastures and semi-natural vegetation, and households, where several domestic predators, such as cats and dogs, are also present. The human population living within the communities neighbouring the reserve was estimated to be about 33,000 people (Muzirambi 2017).

### 3.2. Small mammals' sampling

Rodents were sampled between October and November 2017 (Southern hemisphere summer). Animals were detected using ink tracking tunnels (King and Edgar 1977), left active in the field during four consecutive nights. They consist in tubes made of robust corrugated plastic, with 55 x 10 x 10 cm, allowing rodents to enter. Inside the tube, three sections are considered: both entrances are equipped with an adhesive paper with a glue side up and an ink pad (12 x 10 cm) is placed in the centre (Glennon *et al.* 2002). In the middle of the tunnel, a small PVC pipe section was installed containing bait composed by a mixture of peanut butter, oatmeal and sunflower oil (Hughes *et al.* 1994). The pipe was used to avoid the bait was eaten by the animals entering/crossing the tunnel. The ink tunnels were placed in the ground, grouped in clusters of 9 in a Y-formation, 10 meters apart from each other. The arms of the Y-formation were disposed 120 degrees apart (Figure 3.1b). When visited, the plates of each ink tunnel containing rodent's footprints and tracks were photographed individually after the four days in the field, always at the same distance and with a scale, for further analysis of the data. At the centre of this formation, a camera-trap was placed for the purpose of another study (see preface). Each of the defined ink tunnel clusters were spaced approximately 1.4km apart (Figure 3.1c), considering the average home range of small carnivores and the logistic capacity (M=1.37, SD=0.68, Min=1.02, Max=2.01). In total, were sampled 196 points: 100 points in Phinda, 50 points in the Farms and 46 points in Zulu tribal land.



**Figure 3.2** – Ink tracking tunnel scheme. Above is the ink tunnel seen from the outside, and at the bottom, the removable paper, with an ink pad in the middle.



Rodents' footprints were grouped into two different functional groups according to body length – small (54.4 to 94 mm) and big (107 to 147 mm) rodents. Hindfoot size was estimated for each functional group using Kingdon and collaborators (2013) morphological data. Footprints recorded in track plates had been previously assigned to each of the two functional groups in the frame of another study, using the same data source (Rosa 2019 – Figure 1, Appendix)

Presence data was transformed into relative abundance per sampling point (n° detections/9 ink tunnels), since several studies revealed that such tracking index is positively correlated with abundance measures obtained with live-trapping methods (Wilkinson *et al.* 2012). However, this measure does not allow the identification of footprints up to the species level. Concurrently to the ink tunnel surveys, a live-trapping protocol was implemented in the same three areas as the present study (Rosa 2019). This allowed not only to identify the candidate species that may have used the ink tunnels, but also to validate the ink tunnel surveys, i.e. if the method is capturing relative abundance heterogeneity across the landscape.

### 3.3. Environmental variables collected during the field work.

At the location of each ink tunnel, vegetation type and structure was characterized within a buffer area with 5 meters radius from the tunnel. Characterization was performed according to criteria described by Edwards, 1983 (Table 3.1) and using variables that have been detected as influential to rodents' presence elsewhere (e.g. vegetation height) – (Williams *et al.* 2002; Layme *et al.* 2004; Holland and Bennett 2009). These measurements were taken for each tunnel and then summarized for a sampling point scale analysis. This summary consisted of choosing the most abundant category among the nine tunnels. In case of a tie, the category that made the most ecological sense was chosen, i.e. if there was a tie between open and closed habitat categories, and the remaining categories were semi-covered, the semi-covered category would be chosen because it was an average of the most representative categories. Simultaneously, variables from the camera-traps were recorded (60-90 days), such as capture rate (expressed as the number of independent camera records (> 1 h interval) per 100 trap-days) of cattle, wild ungulates, carnivores, and others (e.g. presence of humans, dogs and cats) used as surrogate of disturbance (Table 3.2). Wild ungulates were grouped in different classes according to their weight, resulting in four categories based on natural breaks in weight values (weight values practically do not overlap), and all cattle (i.e goats and cows) were grouped together in a single variable - Cattle (Table 3.3). Since trampling is one of the negative impacts of ungulates over rodents, I assume that different weights will cause different levels of disturbance.

**Table 3.1** – Environmental variables collected during the field work and used as candidate variables in the modelling procedure. Values represent the percentage (%) of each variable within the 5m buffer centered on the ink tunnel.

Variables	Description	Categories used in the analysis	References
Tree_Cover	% of Tree cover	Continuous (C) – 76-100% Sub continuous (SC) – 51-74% Moderated closed (MC) – 26-50% Semi-open (SO) – 11-25% Open (O) – 0-10%	Martin and Dickinson 1985; Freitas <i>et al.</i> 2000; Layme <i>et al.</i> 2004; Delcros <i>et al.</i> 2015.

Shrub_Cover	% of Shrub cover	Continuous (C) – 76-100% Sub continuous (SC) – 51-74% Moderated closed (MC) – 26-50% Semi-open (SO) – 11-25% Open (O) – 0-10%	Dueser and Shugart 1978; Martin and Dickinson 1985; Dunstan and Fox 1996; Ecke <i>et al.</i> 2002; Delcros <i>et al.</i> 2015; Layme <i>et al.</i> 2004; Kelt <i>et al.</i> 2004.
Grass_Cover	% of Grass cover	Continuous (C) – 76-100% Sub continuous (SC) – 51-74% Moderated closed (MC) – 26-50% Semi-open (SO) – 11-25% Open (O) – 0-10%	Bond <i>et al.</i> 1980; Martin and Dickinson 1985; Monadjem 1997; Layme <i>et al.</i> 2004.
Naked_Soil	% of Naked soil	1 – 76-100% (open) 2 – 51-74% 3 – 26-50% 4 – 11-25% 5 – 0-10% (closed)	Bond <i>et al.</i> 1980; Martin and Dickinson 1985; Dunstan and Fox 1996; Delcros <i>et al.</i> 2015.
Tree_Height	Height of trees	High (H) - >20m Tall (T) – 10-20m Short (S) – 5-10m Low (L) – 2-5m	Dueser and Shugart 1978; Holland and Bennett 2009.
Shrub_Height	Height of shrubs	High (H) – 2-5m Tall (T) – 1-2m Short (S) – 0,5-1m Low (L) – <0,5m	Monadjem 1997; Hoffman and Zeller 2005; Holland and Bennett 2009.
Grass_Height	Height of grasses	High (H) - >2m Tall (T) – 1-2m Short (S) – 0,5-1m Low (L) – <0,5m	Monadjem 1997; Layme <i>et al.</i> 2004; Holland and Bennett 2009; Delcros <i>et al.</i> 2015.

**Table 3.2** – Environmental variables collected during the field work, using camera-trapping, and used as candidate variables in the modelling procedure.

Variable	Description	Mean / Range	Resolution	Source	References
DIST	Distance to houses	2738.97/30.8-9866.9 metres	Collected at point	Camera-trapping survey	Dunstan and Fox 1996.
HUMANS	Capture rate of humans in CT	0.84/0-10	Collected at point	Camera-trapping survey	
DOG	Capture rate of dogs in CT	0.175/0-3.02	Collected at point	Camera-trapping survey	
CAT	Capture rate of cats in CT	0.05/0-0.5	Collected at point	Camera-trapping survey	
Class 1	Capture rate of ungulates	0.397/0-3.04	Collected at point	Camera-trapping survey	Keesing 1998; Hoffman and Zeller 2005; Rautenbach 2013.
Class 2	Capture rate of ungulates	0.651/0-2.90	Collected at point	Camera-trapping survey	
Class 3	Capture rate of ungulates	0.103/0-1	Collected at point	Camera-trapping survey	
Class 4	Capture rate of ungulates	0.119/0-0.83	Collected at point	Camera-trapping survey	

**Table 3.3** – Categories used to describe the abundance of wild ungulates detected during the camera-trapping campaigns. Resulting variables were used as candidate variables in the modelling procedure.

Categories	Species	Weight	References
Class 1	Grey duiker ( <i>Sylvicapra grimmia</i> ), Red duiker ( <i>Cephalophus natalensis</i> ), Suni ( <i>Neotragus moschatus</i> ), Steenbok ( <i>Raphicerus campestris</i> )	4-25kg	Keesing 1998; Hoffman and Zeller 2005; Rautenbach 2013.
Class 2	Nyala ( <i>Tragelaphus angasii</i> ), Warthog ( <i>Phacochoerus africanus</i> ), Impala ( <i>Aepyceros melampus</i> ), Bushbig ( <i>Potamochoerus larvatus</i> ), Common Redbuck ( <i>Redunca redunca</i> )	45-150kg	
Class 3	Zebra ( <i>Equus quagga</i> ), Wildebeest ( <i>Connochaetes taurinus</i> ), Great Kudu ( <i>Tragelaphus strepsiceros</i> ), Buffalo ( <i>Syncerus caffer</i> ), Waterbuck ( <i>Kobus ellipsiprymnus</i> )	120kg-600kg	
Class 4	Giraffe ( <i>Giraffa camelopardalis</i> ), Elephant ( <i>Loxodonta africana</i> ), Black Rhino ( <i>Diceros bicornis</i> ), White Rhino ( <i>Ceratotherium simum</i> ), Hippopotamus ( <i>Hippopotamus amphibius</i> )	800-6000kg	

### 3.4. Variables collected from remote sensing products

I selected remote sensing variables that were highlighted as important to rodents' occurrence in previous studies focused on small mammals: (i) Normalized Difference Vegetation Index (NDVI), which allowed us to describe seasonal variations in vegetation and is therefore widely used as a vegetation productivity proxy (Glass *et al.* 2000; Andreo *et al.* 2009, Mapelli and Kittlein, 2009); (ii) Altitude, slope and terrain orientation, to describe the physical component of the habitat and because influences smaller scale heterogeneity, leading to higher microhabitats diversity (Schulze *et al.* 1997; Venturi *et al.* 2004; Fischer *et al.* 2011); (iii) Land use types and cover (proportion per buffer), allowing to translate landscape complexity (Goodin *et al.* 2006) through the calculation of a diversity index (ex. Shannon); (iv) Land Surface Temperature (LST), defined as the thermal emission of the soil, which varies according to soil cover, with the highest temperatures being registered in areas of bare soil, being a good indicator of the habitat cover structure (Andreo *et al.* 2009).

In total, thirteen predictors (Table 3.4) were selected and data for the study area extracted and stored in a Geographic Information System (GIS). Most of the variables used have the resolution of 30x30m. The Shannon Index was calculated based on a land cover raster with a resolution of 30x30 meters. In order to capture habitat heterogeneity, the Shannon Index was calculated with a coarser resolution than 30x30 meters, resulting in a resolution of 250x250m. This resolution, besides covering at least 5 pixels of the land cover raster allowing to calculate diversity, is a measure that ensure that areas used by individuals for daily foraging activity and small-scale movement are included (Barrett and Peles 1999). The standard deviation of the NDVI (NDVI\_STD) was calculated based on the NDVI. Land use classes (DB, OB, G, CS, UV) were also derived from the land use raster and were chosen because they are the land uses with greater representativeness in each of the study areas (i.e. Phinda Game Reserve, Livestock/Game Farms and Zulu Tribal Land). Buffer zones for land cover classes were described quantitatively through the calculi of the percentage of cover of each habitat feature within each area (Pearson 1993). The resolution of a 75 metre buffer, for NDVI\_STD and land cover classes was chosen for the same reason as described before, but in this case I was able to choose a better resolution to capture

the percentage of habitat and NDVI variation and avoid conflicting with the habitat diversity captured by the Shannon Index (Barrett and Peles 1999).

For categorical variables, histograms were drawn to detect the representativeness of each category within each variable (ex. High for shrubs height). Categories with represented by 5% or less were merged in order to reduce variability introduced in the model.

**Table 3.4** - Environmental variables from geographic information systems (GIS), used as candidate variables in the modelling procedure.

Variable	Description	Mean / Range	Resolution	Source	References
TREE_COVER	% Tree Cover	30.80 / 6-72%	30x30m	Global Forest Watch <a href="https://www.globalforestwatch.org/">https://www.globalforestwatch.org/</a>	Freitas <i>et al.</i> 2000; Delcros <i>et al.</i> 2015.
SHANNON	Shannon Index for Land Cover diversity in a 250m buffer around the cameras.	0.998/0-2,89	250x250m	SASDI <a href="http://www.sasdi.net/">http://www.sasdi.net/</a>	Dunstan and Fox 1996; Williams <i>et al.</i> 2002.
DEM	Digital Elevation Model	66.72/12-204 metres	30x30m	ASTER <a href="https://earthexplorer.usgs.gov/">https://earthexplorer.usgs.gov/</a>	Bond <i>et al.</i> 1980; Dunstan and Fox 1996; Monadjem 1999; Christie <i>et al.</i> 2017.
LST	Land Surface Temperature	33.69/28.87-39.94	30x30m	Landsat 8 <a href="https://earthexplorer.usgs.gov/">https://earthexplorer.usgs.gov/</a>	Andreo <i>et al.</i> 2009.
ASPECT	Aspect, extracted from DEM in QGIS	179.76/2.99-357.32 degrees	30x30m	-	Bond <i>et al.</i> 1980.
SLOPE	Slope, extracted from DEM in QGIS	9.98/0.93-89.99 degrees	30x30m	-	Bond <i>et al.</i> 1980.
NDVI	Normalized difference vegetation index calculated from Landsat images	0.48/0.28-0.67	30x30m	Landsat 8 <a href="https://earthexplorer.usgs.gov/">https://earthexplorer.usgs.gov/</a>	Dueser and Shugart 1978; Miranda 2018.
NDVI_STD	Standard deviation of NDVI in a 150m buffer around the cameras. Measure of production heterogeneity.	0.02/0.006-0.05	75m buffer	-	Dueser and Shugart 1978.
DB	Cover percentage of dense bush/ticket in a 75m buffer	43.22/0-98.44 %	75m buffer	SASDI <a href="http://www.sasdi.net/">http://www.sasdi.net/</a>	Monadjem 1999.
OB	Cover percentage of open bush/woodland in a 75m buffer	14.80/0-77.20 %	75m buffer	SASDI <a href="http://www.sasdi.net/">http://www.sasdi.net/</a>	Monadjem 1999.
G	Cover percentage of grassland in a 75 m buffer	21.47/0-96.92 %	75m buffer	SASDI <a href="http://www.sasdi.net/">http://www.sasdi.net/</a>	Monadjem 1999.
CS	Cover percentage of cultivated subsistence in a 75 m buffer	12.00/0-73.98%	75m buffer	SASDI <a href="http://www.sasdi.net/">http://www.sasdi.net/</a>	Monadjem 1999.
UV	Cover percentage of urban villages in a 75m buffer	7.67/0-98.44 %	75m buffer	SASDI <a href="http://www.sasdi.net/">http://www.sasdi.net/</a>	Monadjem 1999.

### 3.5. Data analyses/modelling

#### 3.5.1. Influence of environmental variables on rodents' abundance

To detect multicollinearity between all independent variables, I estimated the variance inflation factor (VIF) from “fmsb” package (Nakazawa 2018), using the criteria of  $VIF < 5$  for non-collinearity (Ringle *et al.* 2015).

The influence of environmental variables on rodents' relative abundance was tested using a boosted regression trees (BRT) approach, built with the “gbm” package (Ridgeway 2004). This technique encompasses the advantages of regression trees (e.g. predictor variables can be of any type, analysis is insensitive to outliers and can accommodate missing data, Elith *et al.* 2008), overcoming their low predictive capacity through the boosting algorithm. The final model is a linear addition of several regression models in which the simplest term is a tree (De'ath 2007; Elith *et al.* 2008).

BRT models are resilient to model overfitting but, to have a better predictive performance, the model input parameters were defined (Carslaw and Taylor 2009). In BRT, learning rate is the shrinkage parameter that controls the contribution of each tree to the model and tree complexity determines the number of nodes in a tree and consequently its size. These two parameters control the number of trees in the model, while the bag fraction determines stochasticity by selecting the proportion of data being used at each step (Elith *et al.* 2008; Carslaw and Taylor 2009; Williams *et al.* 2010). All models were fitted to allow interactions using a ten-fold cross validation to determine the optimal number of trees for each model. The largest learning rate (lr) and the smallest tree complexity (tc) were selected in order to allow a minimum of 1000 trees in the BRT fitting process (see Elith *et al.* 2008). As the response variable (rodents' abundance) has a normal distribution, analyses were based on a Gaussian function. Non-informative variables were removed during the fitting process, allowing the simplification of the set of variables (Elith *et al.* 2008). That simplification consisted in defining how many variables the function can test to remove, based on relative influence and total number of variables. Then, a graph was produced showing differences in the predicted deviance according to several scenarios, each one with a different number of variables removed. Next, I decided the number of variables to eliminate, and they were removed in order of minor relative influence. The final relative influence of each variable was calculated through a BRT. Relative influence measures are calculated by averaging the number of times a covariate is used for splitting, weighted by the squared improvement to the model as the result of each split. It is then scaled so the values sum to 100 (Colin *et al.* 2017). Fitted values were plotted in relation to the most important predictors, revealing their effects on rodent's abundance. Explained deviance was calculated using the following formula from Abeare (2009).

$$D^2 = 1 - \left( \frac{\text{residual deviance}}{\text{total deviance}} \right)$$

Confidence intervals of 95% were estimated for the fitted function of each variable by taking 500 bootstrap samples of the input data, with the same size as the original data and randomly selected with replacement. A boosted regression tree was fitted to each sample and the percentiles of five and ninety-five were calculated for the points of each function. All analyses were done using the software R Studio Version 1.1.463 (R Core Team 2017; RStudio Team 2015).

Models were implemented for each study area (Phinda, Farms, Rural Communities) aiming to compare the effect of environmental variables in rodent's abundance in the different management areas. To assess the level of the effects of remote sensing variables, I produced BRT models using variables collected at sampling points, and mean values collected in a 75 metres buffer. Those that had higher influence on rodents' abundance, were selected to perform the final model for each group and each area.

This was tested because, since I am working with GIS variables, sometimes the original resolution may not be the scale at which environmental variables affect the organism. In this case, I chose 75 metres according to Barrett and Peles (1999), as referred above. Since abundances meet the assumptions of normality according to Shapiro-Wilk normality test, there was no need to transform the data.

### 3.5.2. Spatial patterns of rodents' abundance across areas and functional groups

Differences in mean abundance and standard deviation values of functional groups according to area (Phinda Game Reserve, Livestock/Game Farms and Zulu Tribal Land) were tested using an ANOVA and, if significant, a Tukey HSD test.

In order to assess the occupancy patterns of rodents' abundance within each area (i.e. aggregate, random/regular pattern), I evaluated the data using Lloyd's Index of Patchiness (Lloyd 1967) for each of the three types of lands with distinct management schemes (i.e. Phinda Game Reserve, Livestock/Game Farms and Zulu Tribal Land). Using the QGIS Landscape Analysis tool (QGIS Development Team), Shannon Diversity Index was calculated for each of the study areas, in order to obtain a characterizing metric of the heterogeneity level.

To identify spatial distribution patterns, gridded maps of each point-centred environmental predictor were developed and interpolated using the Kernel Density Estimation through "as.owin" function from package "maptools" (Bivand *et al.* 2019) and "ppp" and "smooth.ppp" functions from package "spatstat" (Baddeley *et al.* 2019). Remaining variables were already in raster format, so there was no need to interpolate values. All variables were imported to R Studio and then, the fitted BRT model was used to predict the probability of occurrence in the entire study area. A different BRT model was used for each of the management systems, as previously described.

To test if the predicted values were accurate, I tested differences between mean and standard deviation values between original and predicted values, using a Welch Two Sample t-test or Wilcoxon-Mann-Whitney Test if values were not parametric, and Levene Test, respectively.

## 4. Results

### 4.1. Multicollinearity between independent variables

Analysing the Variance Inflation Factor (VIF) for all the independent variables, only Land Surface Temperature showed a value greater than 5 (collinearity) in Farms and Phinda, and was removed from the following analytical procedure. Others were also removed from the analysis, since no spatial variation was detected: Cattle (Phinda), and Class 2 and Grass Height (Rural Communities).

### 4.2. Drivers of abundance

#### 4.2.1. Big Rodents

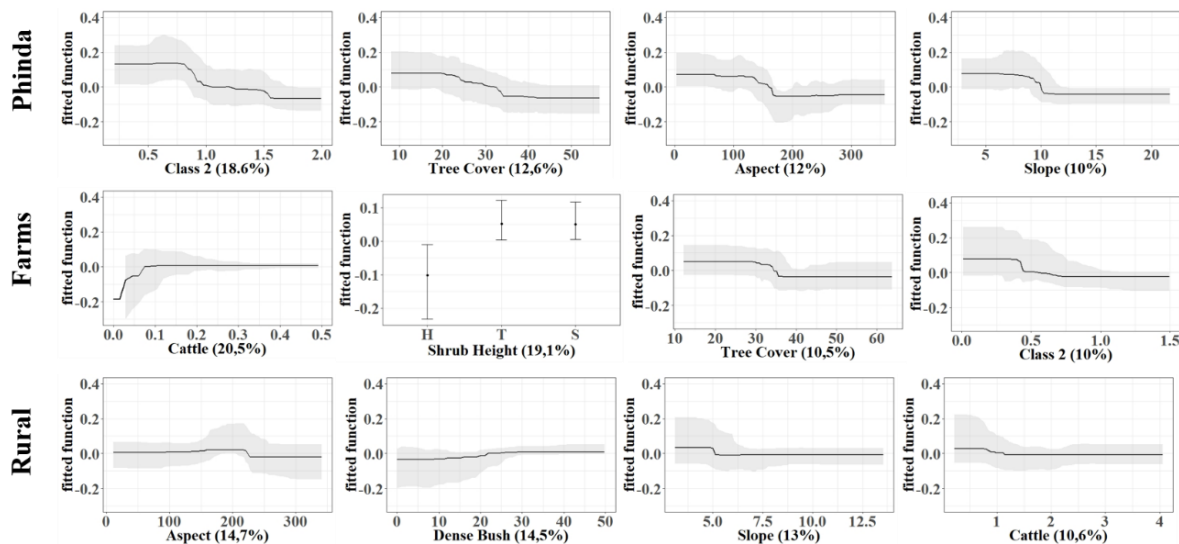
For big rodents, models for Phinda and Farms had a predictive deviance of 54 % and 67%, respectively, indicating a higher model robustness comparing to Rural Communities with just 26%.

In Phinda, the group of variables most strongly influencing abundance were wild ungulates (Class 2), tree cover, aspect and slope (Figure 4.1). Big rodents are, therefore, more abundant where there are low capture rates of wild ungulates, slopes until 10 degrees and oriented east, and tree cover lower than 35%.

For farms, influence of cattle, shrub height, tree cover and wild ungulates (Class 2) was detected (Figure 4.1) on big rodents' abundance. Thus, rodents occur most frequently in areas with lower abundances of wild ungulates, but avoided areas with shrubs over two meters, and with more than 35%

of tree cover. Despite cattle's relative importance being high (20.5%), care must be taken in interpreting these results because the confidence intervals of this variable ranges from positive to negative values, preventing a confident interpretation of the true effect of livestock in big rodents.

Finally, for Rural Communities, drivers shaping big rodents' abundance variation were similar to those identified for the other two areas (Figure 4.1). Aspect and slope had both a negative influence, indicating the same trend previously described. A relation with cattle rises in this analysis as an important factor, but again its confidence intervals range from positive to negative values, hampering the interpretation.



**Figure 4.1** - Function fitted for the most important predictors by a boosted regression tree (BRT) relating the abundance of big rodents to each environmental variable. Three model results are represented, one for each management type area: Phinda Reserve, Farms and Rural Communities. Important predictors are those whose relative importance is above 10%. Confidence intervals of 95% are represented in grey. Functions are continuous for all the variables except for shrub height, that consists in discrete values for each level of the factor predictor (H-high, T-tall, S-small). A common scale is used on the vertical axis for all plots

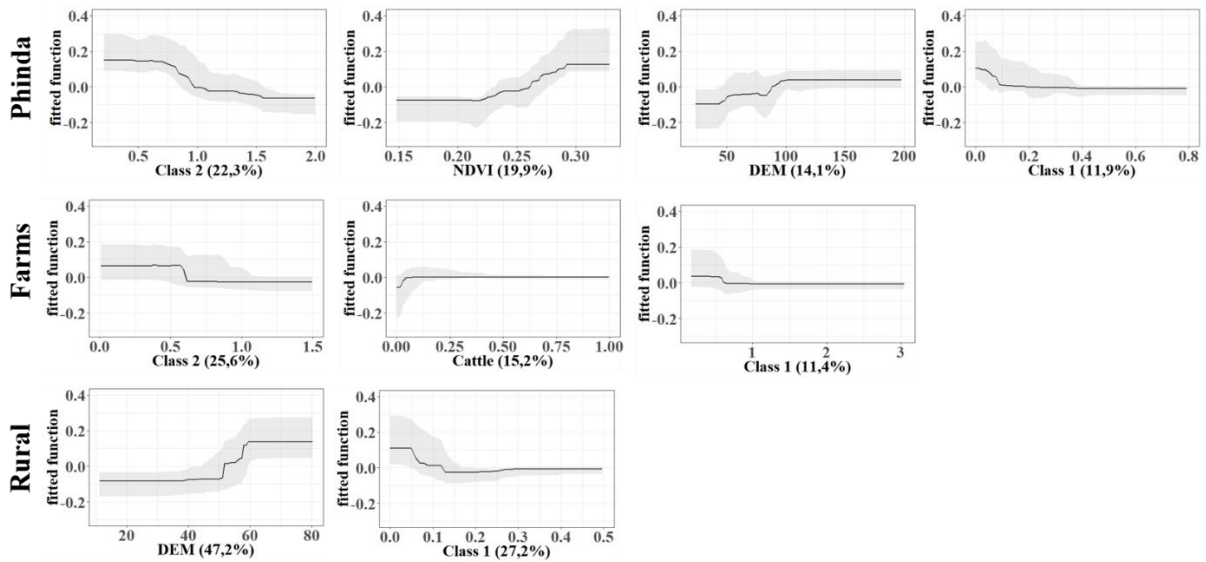
#### 4.2.2. Small Rodents

For small rodents, Rural Communities and Phinda models had the best explained deviance, with 70 % and 52%, respectively. Farms had a lower performance, with only 30%.

In Phinda, small rodents' abundance was again positively influenced by lower capture rates of wild ungulates (both classes). However, NDVI and DEM are also important drivers, with abundance being promoted by high values of productivity (i.e. NDVI) but constrained in lower altitudes (<80m).

For farms, small rodents seem to be influenced by both classes of wild ungulates (Class 1 and 2; Figure 4.2), showing a preference for areas with low abundances. Cattle showed once more a poor performance, with confidence intervals hindering interpretation of the influence pattern (Figure 4.2). For this reason, this variable will not be considered as influential for the farms' dataset.

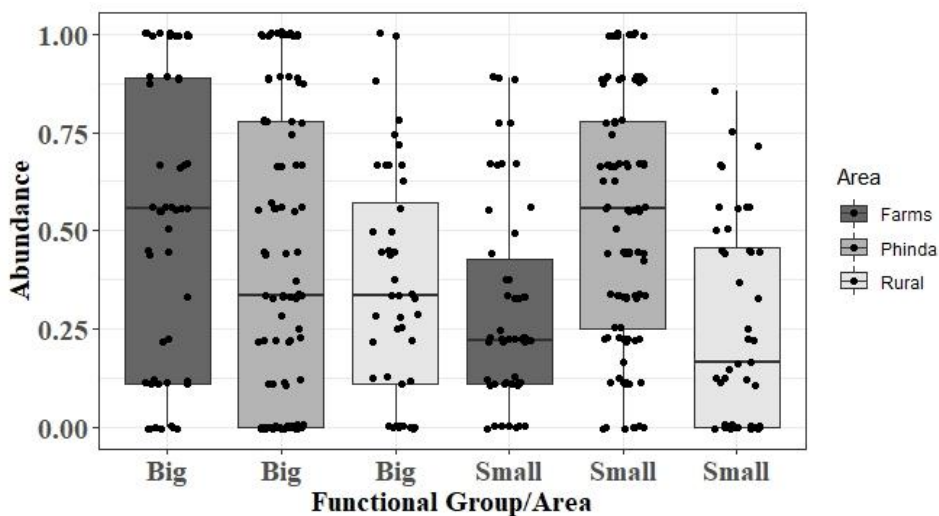
For Rural Communities, the most important variables were once more DEM and wild ungulates (Figure 4.2). Small rodents showed higher abundances in zones with low capture rates of ungulates and above 50 meters of altitude.



**Figure 4.2** - Function fitted for the most important predictors by a boosted regression tree (BRT) relating the abundance of small rodents to each environmental variable. Three models are represented, one for each management area: Phinda Reserve, Farms and Rural Communities. Important predictors are those whose relative importance is above 10%. Confidence intervals of 95% are represented in grey. A common scale is used on the vertical axis for all plots.

### 4.3. Spatial patterns of rodents' abundance across areas and functional groups

Of the 196 sampling points, four had to be discarded from the analysis, due to the disappearance of the cameras or of the ink tracking tunnels (two from Phinda and two from Rural Communities). From the 192 sampling points monitored, 163 presented small rodents' tracks, while 145 had big rodents' tracks, with an overlap in 67 sites. Abundances of both rodents' groups were significantly normal (Small:  $W=0.93$ ,  $p\text{-value}<0.001$ ; Big:  $W=0.88$ ,  $p\text{-value}<0.001$ ). Relative abundances of small and big rodents differed between areas (Figure 4.3). For small rodents significant differences were found between abundances at each of the three study zones ( $F(2,189) = 16.02$ ,  $p<0.001$ ). Post hoc comparisons using Tukey HSD test indicated that mean score for Phinda ( $M= 0.52$ ,  $SD= 0.31$ ) was significantly different ( $p<0.001$ ) than the other two areas (Farms:  $M=0.31$ ,  $SD=0.26$ ; Rural:  $M=0.26$ ,  $SD=0.26$ ), with



**Figure 4.3** - Boxplot of rodents' relative abundance in the three management types zones monitored: Farms, Phinda reserve and Rural Communities.

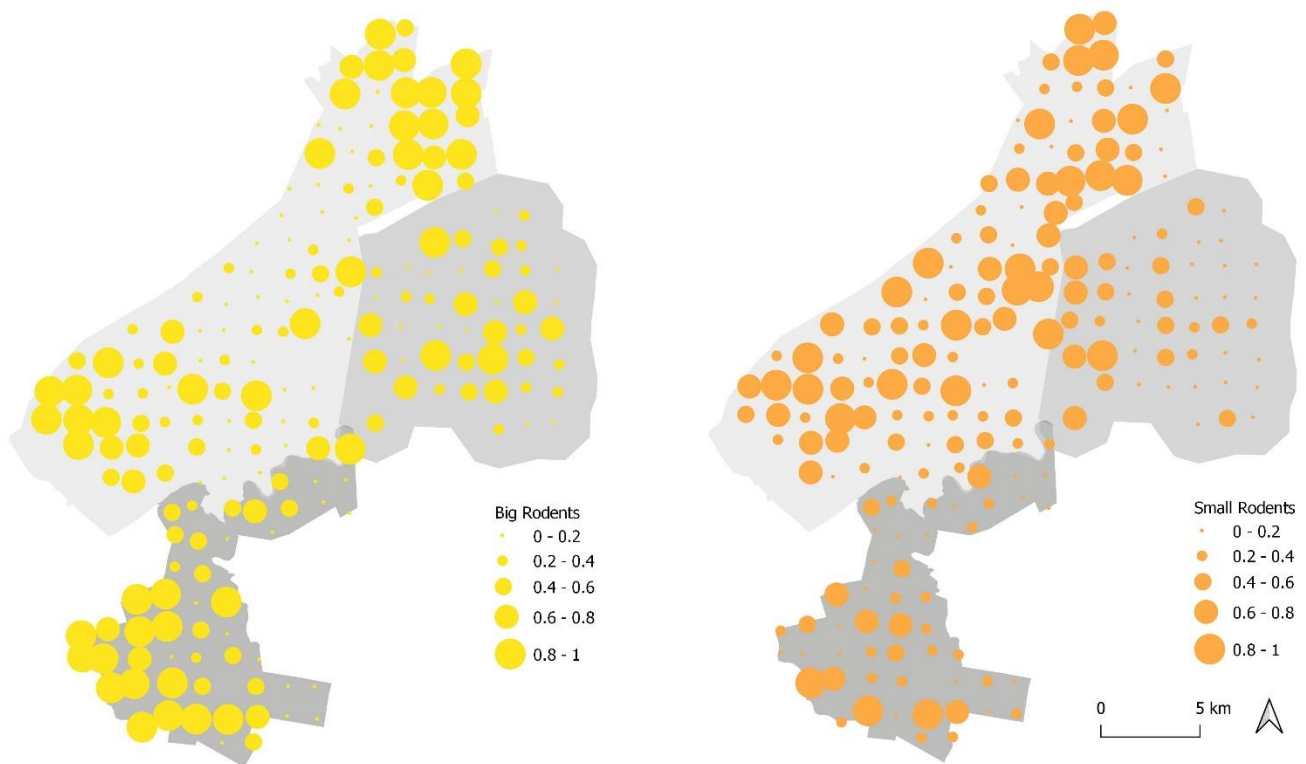


higher abundance values (Figure 4.3). For big rodents no significant differences were found between areas, but farms appear to hold a higher abundance comparing to the other areas (Figure 4.3). Only for Farms, abundances of big (M=0.52, SD=0.37) and small rodents (M=0.31, SD=0.26) were significantly different (p=0.001) Based on these results, each rodent functional group was analysed separately.

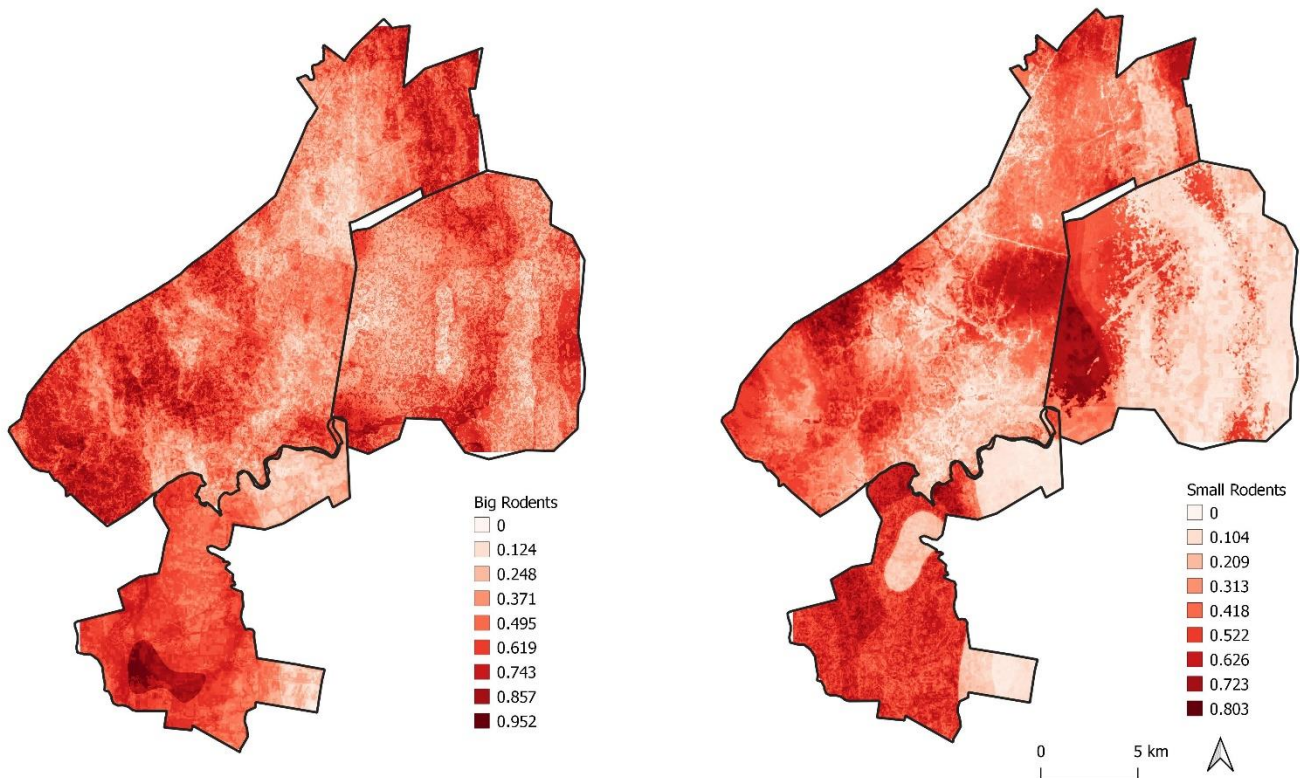
Lloyd's Index of Patchiness revealed that for every area and both groups, rodents' abundance values were significantly aggregated ( $\gamma > 1$ ) as it is possible to verify in Table 4.1. Through Figure 4.4 I intend to illustrate the patterns of rodent abundance, so that it is possible to visualize the areas with the highest aggregation levels of each group.

**Table 4.1** – Results of Lloyd's Index of Patchiness ( $\gamma$ ).

Functional Group/Area	Lloyd's Index of Patchiness ( $\gamma$ )
Small/Farms	1.372
Small/Phinda	1.128
Small/Rural	1.528
Big/Farms	1.296
Big/Phinda	1.529
Big/Rural	1.306



**Figure 4.4-** Map of the study area showing both rodents' distributions: big rodents in yellow and small rodents in orange. The size of each point is equivalent to abundance value, as indicated in the respective legend

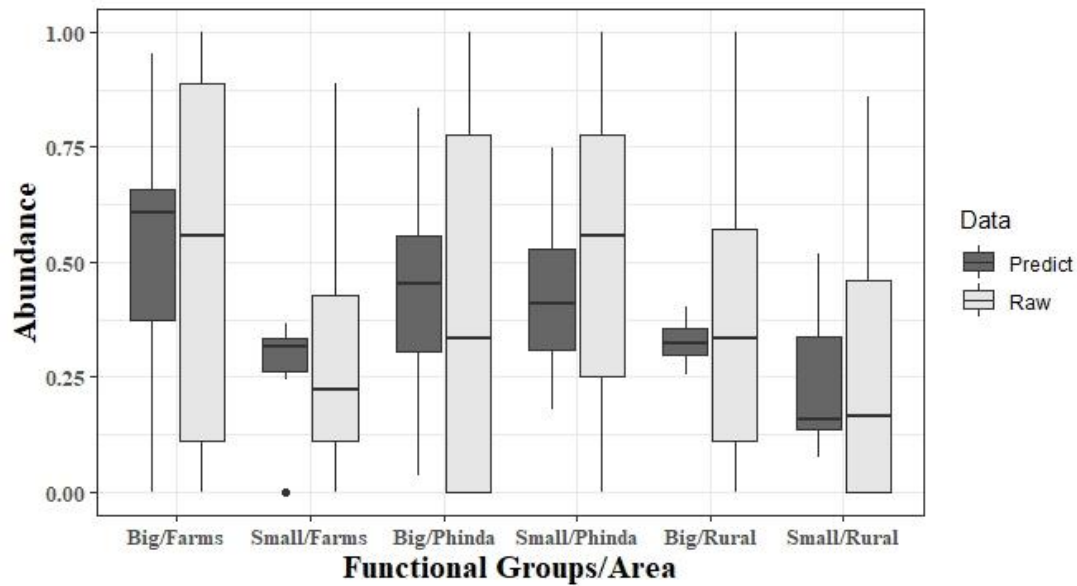


**Figure 4.5-** Map of the study area showing the predicted distribution of both rodent' groups. Different colour shades represent different abundance values (darker =higher abundance), discriminated in the legend above.

The Shannon Diversity Index revealed distinct values for each area, being Phinda the least heterogeneous area ( $H' = 1.19$ ) followed by Farms ( $H' = 1.3$ ) and finally Rural Communities, with the highest values of heterogeneity ( $H' = 2.29$ ).

Although the probability of occurrence of small rodents in Farms and big rodents in Rural Communities is not fully supported by the field data (low model performance), small rodents show an apparent tendency of being more abundant in places where big rodents are less abundant (Figure 4.5). Big rodents are the dominant group in farms while small rodents have an abundance spot in Rural Communities. In Phinda Reserve, the same avoidance pattern is visible.

Comparing predicted values with raw values (original relative abundance), only predicted values for big rodents in Phinda and Rural Communities were not significantly normal, according to Shapiro-Wilk test, therefore comparisons with raw values for these two were through non-parametric Wilcoxon-Mann-Whitney Test (Big/Farms:  $W = 0.89$ ,  $p = 0.0003$ ; Small/Farms:  $W = 0.66$ ,  $p < 0.001$ ; Small/Phinda:  $W = 0.97$ ,  $p = 0.04$ ; Small/Rural:  $W = 0.84$ ,  $p < 0.001$ ). There was only significant differences between mean values of predicted ( $M = 0.42$ ,  $SD = 0.13$ ) and raw abundances ( $M = 0.52$ ,  $SD = 0.31$ ) in Phinda for small mammals ( $t(132.17) = -2.8035$ ,  $p = 0.006$ ). For the contrary, all SD values between predicted and raw values were significantly different (Big/Farms:  $F = 17.85$ ,  $p < 0.001$ ; Small/Farms:  $F = 22.59$ ,  $p < 0.001$ ; Big/Phinda:  $F = 68.75$ ,  $p < 0.001$ ; Small/Phinda:  $F = 66.56$ ,  $p < 0.001$ ; Big/Rural:  $F = 66.05$ ,  $p < 0.001$ ; Small/Rural:  $F = 17.77$ ,  $p < 0.001$ ), as it is visible in Figure 4.6.



**Figure 4.6-** Boxplot representing mean and SD values for functional groups per area, comparing values from prediction and original abundance values (raw).

## 5. Discussion

The present study, focused on the two functional groups of rodents, has shown new evidences for a better understanding of the importance of private ecotourism reserves and game farms for conservation. Responses to variables differ by functional group but were similar between land uses. Although specific models have identified different drivers per areas and rodent's functional groups, a pattern seem to emerge from my analysis: sites with high abundances of ungulates, in general, supported fewer rodents. Furthermore, another pattern is also highlighted, namely that the other influential factors are, overall, directly or indirectly associated with the area's vegetation structure.

### *Drivers of relative abundance*

The present data showed that big rodents' higher abundance is related with higher shrub structure, supporting the first hypothesis (H1). Higher shrubs can provide protection against potential predators (Bond *et al.* 1980; Delcros *et al.* 2015), reducing predation risk, and therefore allowing this group to reach higher abundances. However, small rodents do not show such a clear relation, probably because they can find refuge more easily in other vegetation's structures due to their smaller size. Although important relationships were found, I expected a stronger association with vegetation structure and type, since it is one of the most recurrent factors cited in literature (Williams *et al.* 2002; Layme *et al.* 2004; Holland and Bennett 2009), as it provides shelter, food and microclimatic conditions (Bond *et al.* 1980; Martin and Dickinson 1985; Monadjem 1997). The discrepancy between my results and those elsewhere, can be justified by the fact that in this study I used qualitative vegetation metrics, which limits the discriminant power of variables (Wagner and Gillespie 2018).

Nevertheless, shrubs above 2 metres height influenced negatively big rodents' abundance, which may be associated with vegetation encroachment (Wigley *et al.* 2009). Vegetation encroachment may be caused by a combination of multiple factors. However, overgrazing is an aspect that facilitates the aggravation of this problem (Roques *et al.* 2001; Ward 2005). The intensive removal of grasses increases space availability and soil's moisture, allowing the development of shrubs (Walker *et al.* 1981; Ward 2005). Despite increasing shelter availability, encroachment decreases grass cover and arthropods abundance, therefore reducing food availability (Blaum 2004; Blaum *et al.* 2006). When facing shrub encroachment, small mammals' abundance is mostly determined by food availability than shelter

(Blaum *et al.* 2006), which is in accordance with my findings. The positive effect of low abundances of wild ungulates may be also associated with the same effect (see Figure 4.1 and Figure 4.2, Phinda – Class 2). An experimental study conducted in Kenya showed that vegetation encroachment is controlled by browsers (Pringle *et al.* 2014). Patches with browsers exclusion had higher and well-developed shrubs. In general, ungulates prevent vegetation encroachment, condition of which rodents can benefit, but higher abundances will probably reduce shrubs ability to sheltering rodents.

Topographic features define vegetation type and, therefore, can be used as a surrogate of the habitat structure. The present study showed a clear preference of big rodents for gentle and east oriented slopes. In Hluhluwe-iMfolozi Park, the same relation was found to *Mastomys natalensis*, one of the most common rodent species in South Africa (Russo *et al.* 2016). This relationship can be easily explained by the fact that in the southern hemisphere, dominant winds come from Indic Ocean, what makes east facing slopes wetter/more humid (Osborne 2012). This facilitates the establishment of denser vegetation on these slopes, as opposed to the west-facing slopes, which suffer more erosion and are much drier (Osborne 2012; Russo *et al.* 2016). Thus, these former slopes might be preferred because they host a more humid environment, but also because they can support higher density of vegetation, thus providing better shelter conditions for big rodents.

Another factor to be considered is the relationship between different plant species and the nature of those relationships, an ecological issue widely studied in the African savannas (Scholes and Archer 1997), because of the effect that trees have on grasses' quality, improving their nutritional quality (Vetaas 1992). A study developed in both South Africa and Kenya recorded an elevated foraging frequency by ungulates near trees, due to higher quality of grasses (Ludwig *et al.* 2008; Treydte *et al.* 2010). There is a preference of small rodents for high productive sites in the reserve, and these are possibly associated with trees, since they are the most productive plants. However, I detected an opposite trend for big rodents, since they are negatively associated with tree cover in Phinda and Farms. Although the reasons for such pattern are difficult to disentangle, it should be considered the probably effect of an exclusive competition between small and big rodents, being the big rodents the better competitor (Henttonen *et al.* 1977).

It was not found any evidence of habitat heterogeneity influence in what concerns to rodents' abundance. Habitat heterogeneity was measured using the Shannon Index estimation of land use diversity and the standard deviation of NDVI, as surrogates (see Table 3.4). None of these variables was important according to the developed models, which can mean two things: these variables were unable to capture true habitat heterogeneity or there is no significant heterogeneity at the level of each area. Either way, this information does not support my initial hypothesis (H2) that heterogeneity would have a positive effect on rodent abundance. However, the positive relationship with elevation found for small rodents in Phinda Reserve is the closest clue that I have in my work that habitat heterogeneity can be important to rodents. Though, the altitudinal range between the studied sites are quite small (12m-204m) to determine, by itself, the abundance variation. Such pattern may indicate that there might be another environmental factor that has not been considered in my analysis that is determining the detected relationship. For Phinda, comparing the altitude intervals where small rodents' abundance is higher, with a satellite image (Google Earth), it is possible to confirm that the high abundance area has a rather irregular topography, composed of mountains and valleys, which increases heterogeneity. Higher heterogeneity induces a greater availability of microhabitats and niches (Macarthur and Macarthur 1969; Cramer and Wilig 2002), which increases the species richness and abundance (Fischer *et al.* 2011). In Rural Communities, the altitude variations are capturing a vegetation gradient, with the most important altitude range being located in the least disturbed zone. I believe altitude is capturing indirectly the importance of vegetation structure for these rodents. Contrary to expectations, there was no greater influence of heterogeneity in big rodents compared to small rodents.

The presence of game farming and livestock raising has been found to reduce habitat quality for rodents, since it has been reported to affect the availability of food and shelter (Keesing 1998). This is in line with my prediction (H3), which hypothesise that areas whose management allows a greater number of ungulates would support less abundant communities of rodents. Ungulates are often the main determinant of rodents' abundance, as they are known to negatively influence small mammals in general, due to their impact on vegetation (Keesing 1998). A study conducted in central Kenya showed an increase in small mammals' body weight in the absence of ungulates (Keesing 1998). The study revealed the existence of food competition between ungulates and African rodents because, although being omnivores, they mainly feed on grasses (Iwuala *et al.* 1979). Furthermore, the trampling impacts on small mammals are also a possible explanation for this negative influence, since the soil compaction hampers burrows maintenance (Keesing 1998; Torre *et al.* 2007). Other studies highlighted the impact of a reduction of the herbaceous layer, as it decreases refuge availability and increases predation risk by improving predators' visibility (Tew and Macdonald 1993; Barrett and Pelles 1996; Rohner and Krebs 1996; Torre and Díaz 2004).

Although both groups were similarly influenced by ungulates, it was found that the different classes of ungulates differentially affect the rodent groups under study. While ungulates between 45-150kg (Class 2) influences both small and big rodents, ungulates with less than 25kg (Class 1) only impacts small rodents. One explanation is related to feeding strategies of both ungulate groups. While Class 1 is mainly composed by grazers, Class 2 includes animals that are simultaneously grazers and browsers. Previously I highlighted the importance of shrubs for big rodents, and grasses for small rodents (Monadjem 1997). Thus, big rodents seem to be mainly influenced by browsers, since they consume shrubs, but small rodents are influenced by both grazers and browsers, because they take shelter in both vegetation types. Another possible explanation that is in agreement with the previous one is related to similarities in habitat preferences. Big rodents are negatively influenced by tree cover and prefer more bushy habitats while small rodents select more productive zones (higher NDVI, more trees). Therefore, big rodents prefer more open habitats, while small ones prefer more closed habitats. The species included in the most representative ungulates of Class 2 (Nyala, Warthog and Impala) prefer areas ranging from bush to open savanna, with low trees and thorn shrubs, while the main ungulates of Class 1 (Grey and Red Duiker) have a preference from open grassland to closed woodland (Evans 1979; Fritz 1976; Ben-Shahar and Skinner 1988). This indicates that most ungulates in each group prefer more open habitats for Class 2 and more enclosed habitats for Class 1. Consequently, there is probably overlap in habitat preferences between big rodents and Class 2, and between small rodents and Class 1, being this a possible explanation for the differentiated influence.

Cattle impacts on small mammals seem to follow the same pattern as that detailed for wild ungulates (Bueno *et al.* 2012), although this trend results were not significant. Even if I cannot confidently explain the effect that this variable has on both rodents, it appears to be a positive relationship when cattle occur in low abundances. A possible justification for this pattern may be related with the association of the cattle with the best pasture areas (Ganskopp and Bohnert 2009), as I state in my fourth hypothesis (H4). Cattle's movements are defined by herders, according to the distribution of the best pasture areas and those are probably preferred by rodents too, since their diet consists commonly in vegetable food items (especially green leaves) and also insects and other arthropods (Iwuala *et al.* 1979; Keesing 2000). With the increase of cattle density, a plausible trampling effect may become more influential and the positive effect is diluted and there is no longer a quantified effect by the model.

#### *Abundance patterns variation between areas*

Relative abundance values show that big rodents are more abundant in Farms while small rodents thrive in Phinda (Figure 4.3) but according to Lloyd's Index of Patchiness, big rodents are more aggregated in Phinda and small are more aggregated in Rural Communities, although positive values

for aggregation occurred for the remaining areas. Therefore, we can affirm that the places where rodents occur in greater abundance have the best conditions in most of the area, while sites where they are more aggregated, the areas are more heterogeneous, creating a non-random distribution pattern. For small rodents, aggregation patterns agree with Shannon index heterogeneity values, the more heterogeneous the area, the more aggregated the patterns. However, big rodents prefer Farms above Phinda in terms of abundance and aggregation values. In this case, although Farms have a slightly higher value of heterogeneity, as it is a more irregular area, overall conditions are preferred by big rodents.

Despite these differences, in total, the highest rodent abundance occurs in Phinda and the lowest values occur in Rural Communities. This pattern is in line with results from Shannon-Winner Diversity Index, clearly showing the heterogeneity gradient, where Phinda is the least interventioned/most naturalized habitat, Farms have an intermediate perturbation degree and Rural Communities own the most degraded conditions. All this comes together in the probabilistic distribution map (Figure 4.5) showing that among the three zones being evaluated, Phinda appears to provide the best conditions to rodents, while Rural Communities present the worst conditions overall.

Despite this, Farms proved to be an important area for big rodents. Studies that analysed the influence of protected areas in the conservation of small mammals found that these areas can have negative effects on these taxa, since their conservation aims is mostly focused on wild ungulates and predators (Caro 2011). This induces small mammals' dispersion movements to nearby areas, such as farms and agriculture lands, where they can find resources, while reducing predation and trampling risks. A study conducted in the same studied reserve, revealed a higher abundance of small mammals in adjacent farms and former cattle farms (Rautenbach 2013), in the present study this pattern was only detected for big rodents, since the mean abundance is higher in Farms than in the reserve. In Rosa (2019), the author compared tracking indexes calculated based on ink tracking tunnels and relative abundances calculated with live-trapping data, to see if these measures were related. The results showed that the tracking index for big rodents (medium rodents is how it is referred in Rosa 2019) had higher performance, because it was significantly correlated with relative abundance. The same did not happened for small rodents, having this index a low accuracy compared to the other method. Given that Rautenbach (2013) study was based on live trapping measures, it makes perfect sense that I only had the same result for big rodents, as they are the group whose tracking index most closely resembles to the relative abundance calculated via live-trapping.

In the present study, Farms are a very heterogeneous area, as they cover different types of management, i.e. game farms and cattle farms. However, they are considered areas with good conditions for the survival of rodents, since they provide different sources of food, being the only negative impact the presence of ungulates. In Rural Communities, no active landscape planning and management is implemented. Therefore, urbanization, people and domestic animals (from dogs and cats to cows and goats) coexist in the same place. One of the reasons that can lead to less rodent use of these areas, besides the evident habitat degradation, is persecution by dogs and cats and the poisoning by people. Use of pesticides is quite problematic as rodents are the main food source of many animals, including small carnivores and raptors, which can lead to poisoning by consumption (Ramesh 2015). One of the systems often referred as important to small mammals in Africa, are agricultural systems because they function as food provider patches in times of less abundance or other natural resources (Rautenbach 2013). However, this was not discussed here since the representativeness of these systems is not significant in the study area (CS - Table 3), thus not allowing us to draw any conclusion. As expected, Phinda appears to be the area whose management positively supports the presence of rodents. It is the type of land use less intervention and that has a greater diversity of species, creating a more natural habitat compared to other systems. However, I should stress also the value of Farms for species conservation, as they support a large abundance of rodents.



All these systems form a heterogeneous landscape and are probably interconnected with respect to species maintenance, whereas some species support human intervention better than others. Each one of the studied areas have different management objectives that may enter in direct conflict with small mammal's survival. Farms, as it was previously described, consist in several patches with different land uses, such as cattle raising and game farming. But both land uses have negative impacts on rodents since they both contribute to maintain high abundances of ungulates, wild or domestic. However, for rodents, it appears to be worthwhile the negative impacts, since areas with ungulates have better pastures areas, which is shown by the high abundance of big rodents on Farms. In Rural Communities, conflict is certainly present since rodents are vectors of diseases and crop destruction agents. But high abundances of dogs and cats affect negatively rodents' presence, such as poisoning. Therefore, there is a "natural" control of rodents in Rural Communities. In Phinda, management objectives are focused on big ungulates and predators, species that are valuable in terms of tourism. As it was described before, this have negative consequences for rodents, since ungulates presence increase competition for food. All three management systems include ungulates, which may be wild or domestic, and both end up having negative influence on rodents' abundance, causing heterogeneous patterns. This is in line with my hypothesis (H3) that states that areas with ungulates presence cause rodents to have a heterogeneous distribution. This heterogeneity only reveals itself when rodents' abundance is high enough so that notable differences within the same management area exist, i.e., small rodents are only dominant in Rural Communities, therefore, they only have a notable heterogeneous distribution in this management system.

#### *Abundance pattern differences between functional groups*

Differences in abundance and standard deviation values (Figure 4.3), along with the estimated abundance distribution map (Figure 4.5), allows to highlight that there are considerable differences in both groups' distribution patterns. However, caution must be taken while interpreting these results, since two of the models had a low performance.

Lloyd's Index supports that aggregation levels differ between functional groups, since they preferentially aggregate in different areas (big in Phinda, small in Rural Communities). This pattern do not coincide with the areas with the highest abundance, probably due to differences in the influence scale of environmental variables, which supports the hypothesis that the division into functional groups is a good approach as it evidences variations in ecological requirements, ecosystems functions and relationships.

According to the abundance distribution patterns (Figure 4.4 and 4.5), both rodent's groups occupy the space differently. Big rodents are more abundant in the extremes of the reserve, just as on the west side of Farms, while small rodents abound on the west side of Rural Communities. This reveals that within an area under a specific management approach, habitat quality varies causing a heterogeneous distribution pattern. It is probably the variation of the environmental variables that is causing distinct occurrence patterns in the same area under study, but it can also be a case of niche partition or exclusive competition.

In general, dominant organisms tend to occupy first the best quality habitats, leaving the remaining habitat available for other species (Pimm *et al.* 1985). In this case, since big rodents are the dominant group (Henttonen *et al.* 1977) they occupy the best areas for themselves, leaving the remaining areas available for small rodents. With the prior knowledge that Rural Communities are the most degraded area, big rodents occupied Phinda and Farms best spots, leaving small rodents with the enduring areas. In Rural Communities, small rodents can choose the best places for themselves, as the other group of rodents is mostly absent. Furthermore, since they are smaller, they are more influenced by microhabitat variables and therefore, habitat changes at small scale are sufficient to affect their abundance. Thus, they are able to make the most of rural areas, prevailing in greater abundance in patches, even with lower

size, with better quality. Big rodents are more affected by variables at landscape level, so they only choose the best areas on a larger scale. This appear to represent niche partitioning between the two groups (Shoener 1974) but should be also considered the probably effect of an exclusive competition between small and big rodents, being the big rodents the better competitor (Henttonen *et al.* 1977).

Another likely and interconnected scenario is related to the suitability of each area for each group of rodents. According to my results, big rodents appear to be more influenced by shrubs height in order to have hiding places appropriate to their size. Since Farms are mostly pasture areas, shrubs become a very important hiding place for these rodents. Big rodents are also negatively influenced by tree cover, and since management measures in farms have the objective of maintaining pasture areas, these are selected for big rodents has the preferential area.

Small rodents are positively influenced by NDVI, and Phinda probably has the higher productivity among the three areas (trees). Elevation is another requisite of this group, and the higher/most heterogeneous places, as explained above, are found in Phinda and Rural Communities, since Farms are mostly occupied by big rodents. Therefore, it is possible to see a tendency of big rodents in Farms, and small rodents in Phinda, since the variables that most influence each one of the groups are more present in the respective area where they are more abundant.

#### *Limitations and future directions*

Although for big rodents in Phinda and Farms, and small rodents in Phinda and Rural Communities, the produced models seem to be robust enough to allow us to interpret the detected patters, models produced for big rodents in Rural Communities and for small rodents in Farms revealed to have a low performance. This is clearly showed by the wide confidence intervals of most of the variables' coefficients included in the models that involved positive and negative values, which hampered results interpretation. It seems to indicate that, probably, the variables chosen as candidates for these models did not captured all data variation, leading the model's performance to be quite low.

A study carried out simultaneously, targeting to live trap small mammals, showed that 95% of the catches of the big rodents were of just one species - *Mastomys natalensis* - and more than 95% of the catches of the small rodents were of another species - *Mus minutoides* (see Figure 2, Appendix). Therefore, since through the ink tracking tunnel method, it is not possible to distinguish between species, the patterns found in the present study could be in reality describing the environmental driver of abundance for these two species, instead of a representation of most species from the KwaZulu-Natal small mammal community. However, I believe that my study can contribute to understand what might be determining the abundance of small mammal, representing two distinct functional groups.

Division of rodents into two distinct functional groups, lead to different results between groups since they are affected by distinct environmental factors. For example, each predator has its own metabolism and energy needs, and since available energy is related with prey biomass, prey preferences of small carnivores can vary according to prey size. Assuming that track size is associated with prey size, big rodents are a better energy income that small rodents (Mukherjee *et al.* 2004).

The measure of abundance used was the relative abundance, since several studies revealed that a tracking index is positively correlated with abundance measures obtained with live-trapping methods (Wilkinson *et al.* 2012). However, Rosa (2019) demonstrated that the performance of the track index varied with rodent size showing a low accuracy for small rodents. This may be related to the difficulty of capturing certain species with live trapping (Tanton 1965) and also because some individuals are considered trap-shy. Another possible explanation is that ink tunnels are a less accurate measure for the evaluation of small rodent footprints. Detection probability using ink tunnels is probably better for trap-shy animals, but since it is not possible to identify tracks up to the species level, we never knew exactly what species are being detected. Instead of this tracking index, another possible alternative was to count footprint in order to calculate a visit index, but that would not allow the division into distinct functional



groups and it would be very time consuming, since this is a large scale study. One disadvantage of using ink tracking tunnels is that since small mammals are not trapped, they can visit several ink tunnels, and relative abundance will count them as distinct animals.

The interpolation made with the environmental variables, whose resolution was 30x30 meters, was for a scale whose distance between points is greater than 1km, which may have led to some error in this process. Therefore, mean values of original and predicted abundances were compared statistically. Since there was only significant differences in Phinda for Small rodents, I can assess that the interpolation led to an accurate prediction. Regarding SD values, all are significantly different. Although there is a large discrepancy between the standard deviation values, this deviation is due to the original values being the result of relative abundance based on counts, i.e. values do not vary continuously, as with the predicted values. Therefore, this difference is not due to the poor performance of the model in predicting values, so I can say that the prediction was quite accurate giving the interpolation.

### *Conclusion*

Overall, the present study supports the idea that different functional groups are influenced in distinct ways by land use practices. Sites that bear greater abundances are those that are less disturbed by human management. According to my expectations, Phinda Reserve is the more naturalized system, supporting greater mean abundances of rodents ( $M=0.48$ ), followed by Farms ( $M=0.41$ ) and Rural Communities ( $M=0.31$ ). Rural Communities are the most intervened area, leading to a reduction of the natural habitat heterogeneity, and consequentially, higher fragmentation (Kamusoko 2007). These factors possibly constrained small mammals' abundance due to a variation of the available resources (food and shelter).

Until now, no study assessed the abundance patterns of small mammals considering the division of small African mammals into functional groups, based on size. This approach allowed us to identify distinct drivers of abundance for each group and to have a more global perspective of the distribution of these groups, according to different management strategies of the landscape.

Studies as this are of interest as they help to rethink land use approaches, taking into account resident biodiversity. The results also indicate the need to expand conservation actions to outside protected areas limits, namely to neighbouring areas already modified by man. For biodiversity conservation to succeed in these habitat mosaics, landscape-level policies and management are required to integrate both protected and managed areas, as they also host a large number of species.

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## **GENERAL CONCLUSION**

This study contributes to advance knowledge about the abundance patterns of small mammals' communities that inhabit South African managed landscapes. Furthermore, it also contributes to a better understanding of how different functional groups can be influenced differently by distinct environmental factors. Results also demonstrate that different management goals have distinct effects on the community, being the more renaturalized zones those that promote higher small mammal abundances. Phinda reserve had the higher relative abundance of small rodents, while in Farms big rodents are the dominant group. In Rural Communities, both groups coexist with low relative abundances, since this is the most disturbed area. Rural Communities are areas where cattle roam freely creating inadequate conditions for small mammals' occurrence. Ungulates (wild and domestic) proved to be the main factor affecting rodents' abundance patterns, proving that management measures aiming to promote ungulates need to be reviewed to assure that their populations will not interfere in an irreversible way South African savannas food web through negative impacts on rodents' species (Cameroon and Scheel 2001; McCauley 2006).

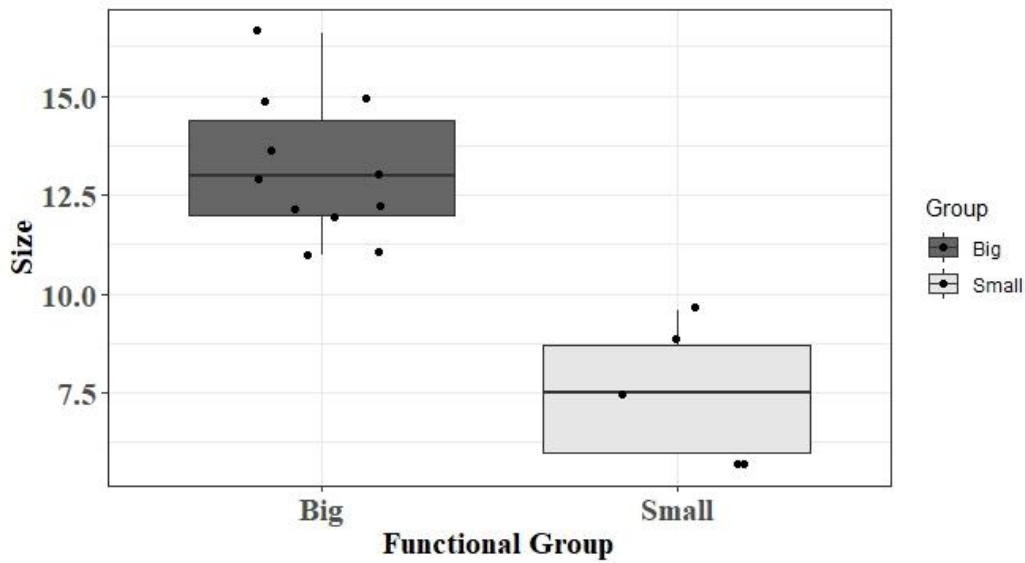
This study has an innovative character because it assesses the different determinants of rodents' abundance in the three main land management types of Austral Africa, using a functional group approach. Considering that land use change is not a trend that is slowing down, it is urgent to understand how small mammals respond to the continuously changing habitats due to man and how we can change attitudes to conserve mammals' species. In the future, it would be interesting to associate variation in prey abundance patterns with mesocarnivores spatial ecology to understand how those can shape carnivores usage of the available landscape elements. It would be then possible to link patterns to the processes shaping those patterns and inform and support decision-making regarding management practices and conservation efforts. In addition, it will also be interesting to do a more thorough analysis of the footprints to improve the methods specificity to distinguish, at least, up to the species of the individuals visiting the ink tunnels. Such improvement will allow monitoring endangered species using a simple to apply, low cost non-invasive methods.

## REFERENCES

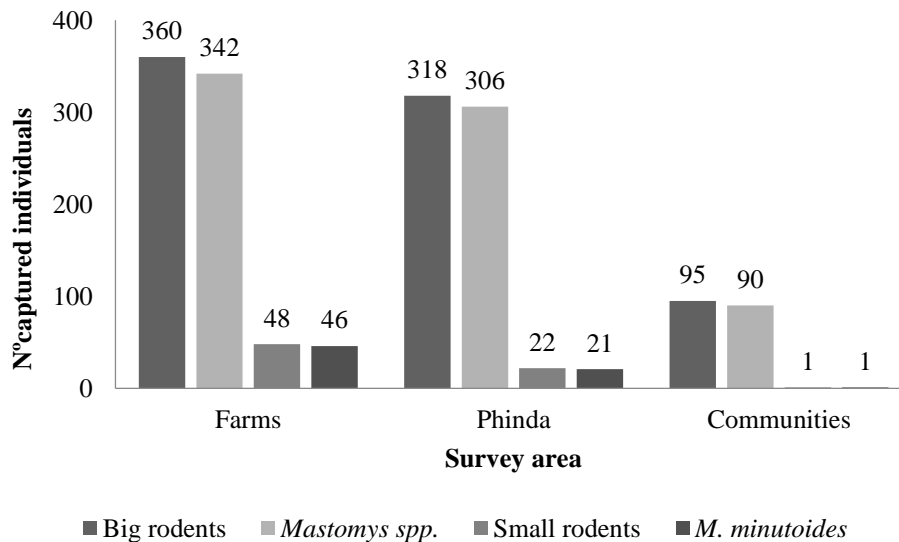
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APPENDIX



**Figure 1** – Boxplot showing functional groups separation, according to a Shapiro-Wilk test. A significant relationship was found between the footprint and the body size, which allowed to state that larger footprints correspond to larger animals. Thus, it was possible to divide small mammals into two distinct categories, small and big rodents, with the threshold at 9 cm length (Figure 2). There was a significant difference in the body size for big (M=13.13 cm, SD=1.3) and small (M=7.56 cm, SD=0.84) rodents;  $t(8) = 6.18, p < 0.001$ .



**Figure 2** –Histogram showing the numbers of big and small rodents captures with live-trapping in relation to the amount of captures of the two most common species for each group: *Mastomys natalensis* for big rodents and *Mus minutoides* for small rodents.