



Role and effects of wild southern African ungulates on seed dispersal of selected alien invasive plants

Lindelwa Msweli

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Role and effects of wild southern African ungulates on seed dispersal of selected alien invasive plants

Lindelwa Sibongakonke Msweli

Submitted in fulfilment of the academic requirements for the degree of

Master of Science

in the Discipline of Ecological Sciences

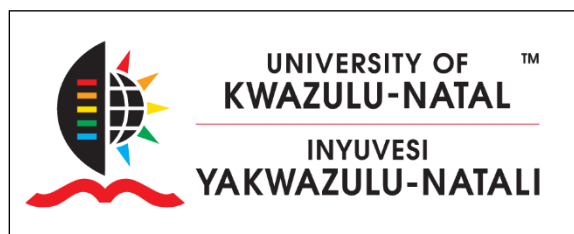
School of Life Sciences

College of Agriculture, Engineering and Science

University of KwaZulu-Natal

Pietermaritzburg Campus

2021



ABSTRACT

Generally, plants species in native ecosystems spread via seed dispersal to potentially establish and promote plant regeneration between communities. However, the introduction of alien invasive plants into indigenous plant communities alters the native ecological process of seed dispersal. Alien invasive plants are considered problematic globally, serving as one of the main threats to biodiversity. Moreover, they have major economic impacts because of management and control initiatives, as well as societal, health and well-being impacts. Consequently, alien plants modify native plant communities, triggering a decline in native habitat availability, and negatively influencing species distribution and composition. Fleshy-fruited alien invasive plants form mutualistic relationships with both native and non-native frugivorous species. These relationships entail providing nutritional rewards from the fruit pulp for frugivorous species, and frugivorous species, in turn, providing a seed dispersal service, thus, intercepting native species interactive relationships between native fleshy-fruited plants and frugivorous species. Therefore, alien invasive fleshy-fruited plants potentially exhibit the greatest detrimental impacts, as their interference in native seed dispersal networks increases their invasion potential. Many African ecosystems are highly invaded by alien invasive plants. However, ungulate species' contribution in seed dispersal, particularly for alien invasive plants, is poorly documented. Because of their large body size, large gut capacity, longer seed retention times and large home range sizes, ungulates potentially serve as primary seed vectors of alien invasive plants. Therefore, understanding ungulate mediated seed dispersal processes is fundamental for the management and conservation of African ecosystems. Our present research aimed to assess the potential contribution of wild southern African ungulate species to seed dispersal of fleshy-fruited alien invasive lantana *Lantana camara*, bugweed *Solanum mauritianum*, syringa *Melia azedarach* and prickly-pear *Opuntia monacantha*. Our objectives were to: (1) determine ungulate visitation and fruit consumption of alien invasive plants; (2) assess the faecal contents of ungulate species to determine seeds of alien invasive plants potentially dispersed; and (3) estimate potential seed dispersal distances of the invasive plants by wild southern African ungulates.

Firstly, we compiled a community of wild southern African ungulates visiting and ingesting the invasive plant species' fleshy fruits using a camera-trapping survey at Fountainhill Estate, Zingela and Nkonka Lodge-Nyala Pans, KwaZulu-Natal, South Africa. The surveys were conducted for 21 consecutive days per camera-trap location. We assessed the strength of

interactions of the wild southern African ungulates with the fleshy-fruited invasive plants, recorded as the frequency of interactions (total number of visitations with and without fruit consumption) and intensity of interactions (total number of visitations with fruit consumption). The results showed that giraffe *Giraffa camelopardalis*, bushbuck *Tragelaphus sylvaticus*, impala *Aepyceros melampus* and greater kudu *Tragelaphus strepsiceros* were the main seed vectors of the fleshy-fruited invasive plants. *Lantana camara* was mostly preferred and ingested by giraffe and greater kudu, and *O. monacantha* by impala and greater kudu. *S. mauritianum* was mostly visited by bushbuck and giraffe; however, no ungulate species were captured ingesting the fruits of *S. mauritianum*. Fruit accessibility by ungulate species was constrained by tree height of *S. mauritianum* and *M. azedarach*, also constraining our data collection and resulted in lesser interactions of *S. mauritianum* and *M. azedarach* than *L. camara* and *O. monacantha*. A higher number of interactions could possibly be obtained by combining camera-trapping with direct observations. Though camera-trapping is a non-invasive technique, direct observations would have been a suitable method in determining the interactions between ungulates and alien invasive plants.

Secondly, we assessed seed composition in the dung of wild southern African ungulates to infer their seed dispersal service for fleshy-fruited invasive plant species at Fountainhill Estate, Zingela and Nkonka Lodge-Nyala Pans, KwaZulu-Natal, South Africa. We simultaneously conducted dung deposition and seed deposition surveys within the respective sites. We intended to quantify and compare seed prevalence in dung piles and predict microhabitats most vulnerable to alien invasions. Dung deposition varied among ungulate species; however, dung of impala and bushbuck were the most common, and common duikers *Sylvicapra grimmia* and zebras *Equus quagga* were the least common. Similarly, dung deposition varied among microhabitats. Habitats that received the highest dung deposition were the savannah and grassland microhabitats. The seed prevalence of alien invasive plants per dung pile varied among ungulate species, sites, invasive plants species and habitats. Overall, dung piles of greater kudu, bushbuck and nyala (*Tragelaphus angasii*) contained the highest number of seeds per dung pile. The lowest number of seeds per dung piles was reported for the common warthog *Phacochoerus africanus* and common duiker, and no seeds of fleshy-fruited alien invasive plants were found in the dung piles of zebra. Across sites, seed composition per dung pile was similar but slightly higher in Zingela and Nkonka Lodge-Nyala Pans. The number of seeds of *S. mauritianum* per dung pile were higher, compared with seeds of *L. camara* and *O. monacantha*. No seeds of *M. azedarach* were found in the dung pile

samples. Savannah and thicket microhabitat received the greatest numbers of seed deposition per dung pile. Dung deposition and seed deposition by wild southern Africa ungulates resulted in a dual confirmation of the savannah microhabitats being the most vulnerable to plant invasions. Conclusively, predicting habitats prone to alien plant invasion is essential for conservation purposes, and maybe potentially used for effective management of alien invasive plants.

Lastly, we estimated potential mean retention times and seed dispersal distances of wild southern African ungulates that ingest fleshy-fruited alien invasive plants and those where these invasive plants were found. We considered body mass (BM, in kg), home range (HR, in km²), and daily movement distance (DMD, in km) of wild southern African ungulates, to estimate potential mean retention time (MRT, in h) and dispersal distance (km) based on allometric equations. MRT (h) varied among ungulate species, firstly based on gut physiology and then on BM (kg). Therefore, even though some hind-gut fermenters (e.g. zebra) were larger in BM (kg) than other ruminant ungulate species (e.g. impala), shorter MRTs (h) were observed for hind-gut fermenters. A strong linearity relationship was observed for both DMD (km) and HR (km²) with BM (kg). Therefore, we estimated potential distances two-fold, based on HR (km²) and DMD (km) as distance proxies. Dispersal distances (km) varied among ungulates, with larger ungulates dispersing seeds further distances than smaller species. Potential dispersal distance using HR (km²) generated a dispersal distance range of 37.45 – 557.22 km, and 45.52 – 248.98 km when using DMD (km), based on BM (kg) of ungulate species. The results showed that although BM (kg), HR (km²), DMD (km) were parameters used to estimate seed dispersal distance, gut physiology is an important factor for modelling dispersal distance of ungulate species. Therefore, when estimating seed dispersal distances, an inclusive approach is obligatory that will incorporate important variables such as gut physiology. However, the allometric equations used to estimate MRT (h) and dispersal distance (km) were shown to be appropriate for the present study. In conclusion, the estimation of MRT (h) and dispersal distance (km) is fundamental for modelling the degree of potential future distributions of alien invasive plants potentially dispersed by ungulate species.

The results obtained from the present study provide vital information for understanding the invasion pathway of fleshy-fruited alien invasive plants through ungulate-mediated seed dispersal. Frugivory interaction of ungulate species and the fleshy-fruited alien invasive plants will assist in understanding ungulate species ingesting, and possibly dispersing seeds of invasive plants. Furthermore, dung deposition and seed deposition outcomes provide insights on seed persistence

per dung pile of ungulates and vulnerable microhabitats for potential plant invasion. Lastly, estimating mean retention time (h) and dispersal distance (km) is essential for understanding the extent to which alien invasive plants may be dispersed. Holistically, the findings provide insight into ungulate species' role in the dispersal of alien invasive plants.

PREFACE

The data described in this thesis were collected in KwaZulu-Natal Province, Republic of South Africa, from February 2019 to September 2020. Experimental work was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Prof Colleen T. Downs and co-supervisor Dr Manqoba M. Zungu.

This thesis, submitted for the degree of Master of Science in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, School of Life Sciences, Pietermaritzburg campus, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.



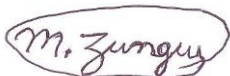
.....
Lindelwa Sibongakonke Msweli
January 2021

I certify that the above statement is correct, and as the candidate's supervisor, I have approved this thesis for submission.



.....
Prof Colleen T. Downs
Supervisor
January 2021

I certify that the above statement is correct, and as the candidate's co-supervisor, I have approved this thesis for submission.



.....
Dr Manqoba M. Zungu
Co-supervisor
January 2021

COLLEGE OF AGRICULTURE, ENGINEERING AND SCIENCE

DECLARATION 1 - PLAGIARISM

I, Lindelwa Sibongakonke Msweli, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs or other information unless specifically acknowledged as being sourced from other persons.
4. This thesis does not contain other persons' writing unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
 - a. Their words have been re-written, but the general information attributed to them has been referenced
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January 2021

COLLEGE OF AGRICULTURE, ENGINEERING AND SCIENCE DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis.

Publication 1

Lindelwa S. Msweli · Manqoba M. Zungu · Christophe Baltzinger · Colleen T. Downs

To eat or not to eat: visitation and fruit consumption of fleshy-fruited alien invasive plants by wild southern African ungulates

Author contributions:

LSM conceived the paper with CB and CTD. CTD sourced funding. LSM collected data, and analysed data and wrote the paper. MMZ provided feedback and guidance on the statistical analysis. MMZ and CTD contributed valuable comments to the manuscript.

Publication 2

Lindelwa S. Msweli · Manqoba M. Zungu · Christophe Baltzinger · Colleen T. Downs

Faecal content composition of wild southern African ungulates: implications for the dispersal of fleshy-fruited invasive alien plants

Author contributions:

LSM conceived the paper with CB, MMZ and CTD. CTD sourced funding. LSM collected data, and analysed data and wrote the paper. MMZ provided feedback and guidance on the statistical analysis. MMZ and CTD contributed valuable comments to the manuscript.

Publication 3

Lindelwa S. Msweli · Manqoba M. Zungu · Christophe Baltzinger · Colleen T. Downs

Potential mean retention time and seed dispersal distances of alien invasive plants by wild southern African ungulates

Author contributions:

LSM conceived the paper with CB, MMZ and CTD. CTD sourced funding. LSM collected data, and analysed data and wrote the paper. MMZ provided feedback and guidance on the statistical analysis and modelling components. MMZ and CTD contributed valuable comments to the manuscript.



Signed:

Lindelwa Sibongakonke Msweli

January 2021

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to share this moment with me, my deceased maternal grandparents: my grandfather Prince Caiphas B. Mkhwanazi of Khula Village and Shikishela Village in Mtubatuba, an ‘uneducated’ but selfless and intelligent leader full of wisdom, I carry your legacy within me; and my grandmother Mrs Hilda S. Mkhwanazi, your spiritual journey and faith in Christ Jesus is a story I hope to share with my own children and grandchildren one day, I carry your spiritual wisdom within me. I extend my deepest gratitude for the spiritual support from my dear friend Thembelihle Ngema; and my family in Christ, my pastor MV Nkomonde, Mr Sipho and Mrs Nothile Zulu, and Zintle Makehle, your fruitful prayers do not go unnoticed. To my prayer partners Thembelihle Ngema, Mrs Nothile Zulu and Zintle Makehle; your intercessions on my behalf have carried me through to the finish line. I would also like to thank anyone who assisted and supported me in any form or another but not mentioned above; you are highly valued.

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“For I know the plans I have for you”, declares the LORD, “plans to prosper you and not to harm you, plans to give you hope and a future.” (Jeremiah 29:19)

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ABBREVIATIONS AND ACRONYMS

BM	Body Mass
DFFtE	Department of Forestry, Fisheries, and the Environment
DMD	Daily Movement Distance
FHE	Fountainhill Estate
GPS	Global Positioning System
HR	Home Range
KZN	KwaZulu-Natal
MCP	Minimum Convex Polygon
MRT	Mean Retention Time
NEM:BA	National Environmental Management: Biodiversity Act
NLNP	Nkonka Lodge – Nyala Pans
SDE	Seed Dispersal Effectiveness
USD	United States of America Dollar
WfW	Working for Water
ZAR	South African Rand

CHAPTER 1

Introduction

1.1 Alien invasive plant species

Alien invasive plants are non-native species that are transported out of their native range (Rejmánek, 1995; Burns et al., 2019) and become problematic in plant communities of the newly invaded regions (Hui and Richardson, 2017). Although invasion biology is a natural phenomenon (Rejmánek, 1996), accelerated rates of alien invasions are experienced globally because of species displacement and redistribution attributable to humans' rapid commercial movement (Reaser et al., 2007; Rejmánek et al., 2013; Fernandes et al., 2019). The bulk contribution of human-initiated direct introductions of alien plant species occurred from the 1600s during the European colonial era (Hui and Richardson, 2017) and the Portuguese trade era (Zimmermann et al., 2004; Olckers, 2011). These extensive global explorations were significantly characterised by colonial trading of goods (Hui and Richardson, 2017), including flora that have become invasive species over time (Zimmermann et al., 2004; Pratt et al., 2017).

Alien plants possess attributes that facilitate their invasion fitness, i.e. invasion capacity, the ability for alien invasive plants to thrive in newly introduced regions (Dutta, 2018; Thompsons, 1991). These characteristics include early germination patterns, rapid growth (Gioria and Pyšek, 2017), and weedy characteristics (Rejmánek, 1995) that initially permit for growth in disturbed habitats that are undesirable by native plant species (Hobbs, 1989; Mooney and Hobbs, 2000). The enemy release hypothesis postulates that invasive alien plants experience an increased distribution and abundance because of reduced control by natural enemies in the newly introduced region (Kaene and Crawley, 2002). Thus, over time, these alien invasive plants effectively breed and become naturalised (Richardson et al., 2000; Hui and Richardson, 2017). The capabilities of

reproducing offspring and dispersing seeds permit alien invasive plants to form part of the native environment (Richardson et al., 2000). However, invasion capacity is contingent upon the characteristics of alien invasive plants at the initial phase of the invasion process and on population size and ecosystem vulnerability of the newly invaded region (Dutta, 2018).

Not all alien plants become invasive (Rejmánek, 1995), but potentially may become invasive in the future (Yemshanov et al., 2019). Some alien plant species have failed to successfully invade new habitats (Hui and Richardson, 2017); however, proper assessments are significantly limited in the literature (Rejmánek and Richardson, 1996). Some alien invasive plants have faced the discriminant and flawed process of classification and have been previously classified as non-invasive (e.g. *Melia azedarach*) (Rejmánek, 1995), potentially constraining and limiting the early management and control action against these plant species (Yemshanov et al., 2019; Bitani et al., 2020). This may be the case for alien plants that are not yet invasive, consequently requiring the same management and control practices as plants already classified as alien invasive (Henderson, 2001). The long-term success of alien plant management is largely dependent on the degree of indigenous ecosystem recovery post-management, as ecosystems are prone to re-invasion, thus the large seed bank because of copious seed production by some alien invasive plant species (e.g. *Solanum mauritianum* and *Lantana camara*) hinders restoration efforts (Holmes et al., 2005). Nevertheless, globally the establishment of alien invasive plants challenges biodiversity conservation initiatives (Richardson and van Wilgen, 2004; Dutta, 2018) and does not only negatively impact ecological systems but also have economic and societal consequences (Davies et al., 2016; Bartz and Kowarik, 2019; Bitani et al., 2020).

1.2 Impacts of alien invasive plant species

Alien invasive plants are a major threat to biodiversity (Higgins and Richardson, 1996; Wilson et al., 2013; Ruwanza and Shackleton, 2016). Ecologically, alien invasive plants modify native communities, triggering ecosystem modification and biodiversity loss (Mack, 1985; Thompson, 1991; Fratte et al., 2019), eventually causing a decline in native habitat availability (Traveset and Riera, 2005). Moreover, they negatively influence species distribution and composition (Gaertner et al., 2009; Vilá et al., 2011), thereby affecting native species interactive relationships (van Wilgen et al., 2008; Ramaswami et al., 2016; Martin-Albarracin et al., 2018). Invasive plants jeopardise ecosystem functioning and stability (Richardson and van Wilgen, 2004; Davies et al., 2016) by adjusting abiotic processes such as biogeochemical cycles, affecting nutrient recycling and soil chemistry by releasing chemical compounds into the soil (Ehrenfeld, 2003; Dassonville et al., 2008). For example, *L. camara* releases allelopathic chemicals that suppress the growth of native plants in its vicinity (Henderson, 2001; Traveset and Richardson, 2006). However, the vulnerability of ecosystems to plant invasion differs across habitats, influenced by resource availability and disturbance level (Daehler, 2003; Pyšek and Richardson, 2010; Dutta, 2017), particularly anthropogenic disturbances (Dutta, 2018).

The biodiversity of a country provides numerous ecosystem goods and services (Le Maitre et al., 2000; de Groot et al., 2002; Richardson and van Wilgen, 2004; van Wilgen et al., 2008) essential for forest production, fisheries and agricultural industries, biological diversity, human health and livelihoods (Millennium Ecosystem Assessment, 2005). However, ecosystems severely impacted by invasive plants inevitably declines in ecosystem service provision (Pimentel et al., 2005; Pejchar and Mooney, 2009; Shackleton et al., 2019a), thus impacting economies of countries (van Wilgen et al., 2008; McConnachie et al., 2012; Shackleton et al., 2019b). This occurs because

of substantial costs in management and control initiatives (Higgins and Richardson, 1996; Richardson and van Wilgen, 2004; Pimentel et al., 2005; van Wilgen et al., 2008). Countries worldwide spend millions to billions of USD on alien invasive plant control programmes (Pyšek and Richardson, 2010; Wilson et al., 2013, 2017), which are often ineffective (McConnachie et al., 2012; van Wilgen et al., 2012). The impacts of ecosystem service provision by invasive plants have received noticeable attention and documentation, especially in developed countries (Mooney and Hobbs, 2000), though certain ecosystem services have been less prioritised than others (Duncan et al., 2004). Moreover, developing countries have received less impact evaluation of alien invasive plants on ecosystem service provision (Nghiem et al., 2013; Peh, 2010). In developing countries, alien plants are one of the main drivers of socio-economic and socio-ecological impacts that threaten societal well-being and livelihoods (García-Llorente et al., 2008; Shackleton et al., 2019b).

More significantly, this is in the case of rangeland degradation, where the grazing ecosystem provision is an important service for subsistence agriculture and livestock farming (Nghiem et al., 2013; Nkambule et al., 2017; Pratt et al., 2017). Globally, most agricultural crops are non-indigenous species, deliberately introduced for food security, and important for national economies (Sharma et al., 2010; Stafford et al., 2017); however, non-agricultural alien plant species (e.g. *L. camara*, *S. mauritanum*, *Opuntia monacantha*) frequently reduce crop yield and are toxic to livestock, therefore impacting food security (Pimentel et al., 2005; Nkambule et al., 2017). Comprehensive quantitative data on economic and societal impacts by alien invasive plants is not well documented (Pejchar and Mooney, 2009) relative to ecological impacts (Bacher et al., 2018). Therefore, establishing predictive guidelines for identifying potential alien plant species with the greatest invasiveness capacity (Rejmánek and Richardson, 1996; Moshobane et al., 2019),

and using early detective strategies (Yemshanov et al., 2019), holistically based on ecological, social and economic impacts (Measey et al., 2016) is fundamental for effective alien invasive plants management and control (Pyšek, 2001; Sutherland, 2004; Bitani et al., 2020).

1.3 Role of seed dispersal in the spread of invasive alien species

1.3.1 Endozoochory seed dispersal

The immobility characteristic of plant species has established an evolutionary interactive plant-animal relationship to enable their movement and dispersal (Vázquez and Aizen, 2004; Muñoz et al., 2016). Seed dispersal, the transportation of seeds away from the parent-plant (Janzen, 1984; Pakeman, 2001; Baltzinger et al., 2019), facilitates population regeneration and maintenance in plant communities (Rey and Alcantara, 2000; Wilson and Downs, 2012). Frugivores use adaptive dispersal mechanisms (Baltzinger et al., 2019), such as endozoochory, which pertains to the ingestion of fruits (Janzen, 1984), for seeds to be eventually regurgitated or defecated by frugivores elsewhere (Wenny, 2001; Prasad et al., 2006; Jordaan et al., 2011a). Avian species are documented as the main endozoochory seed dispersers likely because of the amount of research invested in these species (Murray, 1988; Levey et al., 2005; Jordaan et al., 2011b; Thabethe et al., 2015a; Gioria and Pyšek, 2017). Other vertebrate frugivorous species that are endozoochory seed dispersers include primates (Chapman, 1989; Wall, 1994; Garber and Lambert, 1998; Slater and du Toit, 2002), rodents (Forget and Milleron, 1991; Forget, 1990; Cosyns et al., 2005b), bats (McConkey and Drake, 2006; Jordaan et al., 2012), and large mammals, such as ungulates (Cosyns et al., 2005a; Couvreur et al., 2005; Picard et al., 2015; Pellerin et al., 2016). In tropical and sub-tropical regions, about 90% of plant species partake in plant-animal dispersal interactions, such as endozoochory seed dispersal (Howe and Smallwood, 1982; Jordano, 2000; Dugger et al., 2018),

with the majority of plant species characterised by fleshy fruits (Howe and Smallwood, 1982; Wilson and Downs, 2012). Therefore, the seed-frugivore interactions for seed dispersal purposes highlight the importance of seed vectors in spatial distributions of plant species (Dugger et al., 2018), and their role in ecosystem functioning (Schleuning et al., 2015), especially in indigenous plant communities (Jordano et al., 2007; Wilson and Downs, 2012). However, seed-frugivore interactions form dynamic and complex dispersal networks and are difficult to assess at temporal and spatial scales (Schleuning et al., 2015; Dugger et al., 2018), resulting in generalised interactions at community-wide level (Bascompte et al., 2003; Bascompte and Jordano, 2014).

Seed dispersal does not merely facilitate the transfer of seeds (Campos et al., 2016, 2018; Sridhara et al., 2016). The movement of offspring seeds away from the parent plant may potentially result in higher chances of seedling establishment (Howe et al., 1985; Muñoz et al., 2016) for the colonisation of vacant habitats (Janzen, 1984). Moreover, dispersal of seeds away from conspecifics reduces intraspecific competition (Nathan and Muller-Landau, 2000; Milotić and Hoffmann, 2016). In addition, seed dispersal allows for genetic flow among distant plant populations (Schupp et al., 2010). Moreover, factors such as fruit characteristics (Bruun and Poschlod, 2006; Kuprewicz, 2013; Corlett, 2017), gut passage physiology (Picard et al., 2016; Pellerin et al., 2016), seed retention time within the gut passage (Jordaan et al., 2011a; Mouissie et al., 2005b; Dlamini et al., 2018), frugivore movement patterns and dispersal distances (Sutherland et al., 2000; Will and Tukernberg, 2008; Côrtes and Uriarte, 2013; Rehm et al., 2019), the condition of microhabitat at seed deposition site (Traveset and Verdú, 2002; Schupp et al., 2010, 2017), seed traits and germination patterns (Traveset et al., 2007; Mokotjomela et al., 2015; Thabethe et al., 2015a; Gioria and Pyšek, 2017) collectively contribute to the effectiveness of seed dispersal of plant species.

1.3.2 Seed dispersal effectiveness

For seeds to be effectively dispersed, successful seedling establishment is necessary (Schupp, 1993; Schupp et al., 2010; Schupp et al., 2017). Seed dispersal effectiveness (SDE) estimates the contribution of seed vectors and seeds to the ultimate success of dispersal (Schupp and Fuentes, 1995). The numbers of animal visitations to fruiting plants and fruits consumed per visit are crucial subcomponents when determining the quantitative component of SDE (Schupp et al., 2010; Schupp et al., 2017), elucidating the number of seeds an animal can disperse at a given time (Vázquez et al., 2005). Thus, the quantitative component of SDE determines the seed-frugivore visitation interaction (Schupp, 1993; Campos et al., 2018), consequential for the probability of seed movement. Once fruits are consumed, treatment of seeds in the mouth and gut of frugivores (Whitney et al., 1998; Schupp et al., 2010) and quality of seed deposition microhabitat explains the quantitative component of SDE (Jordano and Schupp, 2000), which informs seedling germination and growth to maturation (Schupp et al., 1989). Ultimately, SDE is quantified using the quantitative and qualitative aspects of seed-frugivore interactions, as the probability of seed establishment given the number of seeds dispersed (Schupp, 1993; Schupp et al., 2010; Schupp et al., 2017). Though the subcomponents are autonomous from one another, each contributes and influences the SDE of plant species (Jordano and Schupp, 2000).

Seed-frugivore interactions are dynamic, forming complex dispersal networks that are difficult to quantify (Schleuning et al., 2015; Dugger et al., 2018) because of the variability of both seed traits (Howe and Smallwood, 1982; Bruun and Poschlod, 2006) and seed vector behavioural and physiological traits (Kleyheeg et al., 2017). Both SDE components are equally vital; however, the effectiveness of seed dispersal is highly dependent on the quantitative component rather than

the qualitative (Schupp, 1993; Mokotjomela et al., 2015). Quantitatively, SDE may be compromised because of reduced numbers of visits to fruiting plants resulting in fewer seeds potentially dispersed (Traveset, 1998; Schupp et al., 2017). Qualitatively, SDE is further compromised because of seed damage by frugivory at ingestion or in the gut (Snow, 1971; Schupp et al., 2010) and the unfavourable microhabitats where seeds are deposited, influencing germination (Lamprey, 1967; Traveset et al., 2007; Fontúrbel et al., 2017). Moreover, SDE may vary depending on the frugivore type, as animals may interact differently from one another with plants (González-Castro et al., 2015; Sridhara et al., 2016). Although direct focal observations are the better tool for studying plant-animal interactions, camera-traps have been used as a non-invasive technique to monitor endozoochory frugivory interactions (Prasad et al., 2010; Bridges and Noss, 2011; Campos et al., 2016; Campos et al., 2018), to quantify quantitative component of SDE, thus suitable for investigating animal visitation and fruit consumption.

1.3.3 Effects of fruit characteristics on invasiveness

Numerous studies have shown that fruit choice by frugivorous species is considerably influenced by several fruit characteristics such as fruit type, fruit size, seed size and seed load, fruit nutritional content, fruit secondary compounds, and fruiting season (Herrera, 1987; Herrera, 2001; Izhaki, 2002; Gosper et al., 2005; Buckley et al., 2006; Gosper and Vivian-Smith, 2009, 2010; Jordaan and Downs 2012a, 2012b; Jordano, 2014; Thabethe et al., 2015b). Most alien invasive plants are characterized by a fleshy fruit type (Cronk and Fuller, 1995; Jordaan et al., 2011a), offering frugivores fruit pulp with higher nutritional content than native plant species (Gosper and Vivian-Smith, 2010; Ramaswami et al., 2016). However, fruits differ in their energy reward (Gosper and Vivian-Smith, 2010; Jordaan and Downs, 2012b). Consequently, the mutualistic relationship

between fleshy-fruited invasive plants and frugivorous dispersers results in a nutritional reward for frugivores, and dispersal service for seeds (Gosper and Vivian-Smith, 2009, 2010; Wilson and Downs, 2012; Zungu and Downs, 2017). Furthermore, the fleshy fruits contain small-sized seeds (Gosper et al., 2005; Bitani et al., 2020), often with copious seed production, with seeds persisting in the seed bank for longer periods (Witkowski and Garner, 2008; Martin-Albarracin et al., 2018). In southern Africa, small-seeded invasive alien plants that originate from the Americas region generally have longer fruiting seasons, such as *L. camara* and *S. mauritianum* (Bitani et al., 2020). Moreover, these typically have fruiting periods that persist beyond the fruiting season of native plant species (Gosper and Vivian-Smith, 2010). As a result, these invasive plants become readily available as a food source for frugivorous species, thus intercepting native dispersal networks (Ramaswami et al., 2016; Martin-Albarracin et al., 2018). Hence, invasive alien plants' fruit traits facilitate an increased degree of invasiveness revealed by the enhanced seed-frugivore dispersal interaction of dispersers with invasive plants (Thompsons, 1991; Buckley et al., 2006). Ultimately, the competitive advantage of alien plants explains their robust invasion efficiency.

1.3.4 Effects of seed dispersal agent behaviour

Frugivorous species are important for dispersing a variety of fruit types of different plant species (González-Castro et al., 2015; Sridhara et al., 2016). Once fruits are ingested, frugivorous species exhibit different adaptive behaviours that contribute to the displacement of seeds. The displacement of seeds includes all behaviours that potentially dictate where seed deposition sites occur, encompassed by the quality variables of SDE (Schupp, 1993; Schupp et al., 2010). Seasonal and daily activities of frugivores highly influence seed deposition site occurrence; however, ultimately, seed vector movement patterns are fundamental for the distance, density and

distribution of dispersed seeds (Côrtes and Uriarte, 2013). Frugivore movement patterns and dispersal distances ultimately denote their contribution to the displacement of seeds away from the parent plant (Sutherland et al., 2000; Will and Tukernberg, 2008; Côrtes and Uriarte, 2013; Rehm et al., 2019). Animal movement patterns may be studied using a variety of methods, from the primitive method of studying dung deposition (Welch, 1982; Putman et al., 1991), varied global positioning system (GPS) tracking technologies (Tomkiewicz et al., 2010), to the correlated models for random movement (Borger et al., 2008; Mouissie et al., 2005a; Smouse et al., 2010). Despite varying in their accuracy, all methods give an account of habitat-use and selection patterns (Côrtes and Uriarte, 2013). Movement patterns and dispersal distances vary among frugivores, usually associated with a variation of intrinsic and extrinsic factors, including social organization and mating systems (Karubian and Durães, 2009), body mass, gut physiology, seed retention time and home ranges (Rehm et al., 2019). The factors are important aspects in determining the patterns of seed dispersal. Frugivore movement patterns are confined by home range size, therefore determining the extent to which seeds may be potentially dispersed (Côrtes and Uriarte, 2013). Within their home ranges, habitat structure and composition can determine direction, length and speed of movement (Moorcroft and Barnett, 2008). However, to predict seed dispersal patterns, an understanding of how extrinsic factors affect intrinsic factors and how both influence movement and seed deposition patterns (Cousens et al., 2010; Côrtes and Uriarte, 2013).

1.3.5 Effects of seed traits and gut passage on germination patterns

Seed ingestion by frugivorous species is a vital element in the facilitation of seed dispersal (Janzen, 1984; Traveset, 1998) via the gut passage of frugivorous species (Bruun and Poschlod, 2006). The gut passage promotes accelerated seed germination (Traveset and Verdú, 2002; Milotić and

Hoffmann, 2016; Kleyheeg et al., 2018). Ingested seeds that survive the gut passage and are not damaged in the mount during chewing or completely digested and are later defecated in a suitable environment for germination may potentially experience enhanced germination, which is enabled by (1) gastric scarification of the seed coat, (2) gastric disinhibition by the removal of pulp, and (3) seed fertilisation by dung material (Traveset, 1998; Traveset and Verdú, 2002; Traveset et al., 2007). The evidence of gastric scarification of the seed coat is achievable by comparing seeds that have passed through the gut passage with those that have not, in their germinability (an increased germination rate post gastric) (Traveset et al., 2008) and seed coat transformations post gastric (a decrease in seed coat thickness) (Traveset et al., 2001). Fruit pulp contains enzymes that inhibit germination while the seed is within the fruit; therefore, ingestion of a fruit separates the seed from the fruit pulp, allowing germination (Traveset et al., 2007). Many studies have compared germination rate between seeds and whole fruits, concluded a much lower germination rate of seeds within whole fruits (Jordaan et al., 2011a, 2011b; Dlamini et al., 2018). Lastly, at seed deposition sites, the dung material may serve as a fertiliser for the seed, enhancing germination (Traveset and Verdú, 2002).

Research has shown that seed germination depends not only on the involvement of frugivorous species for gut passage treatment but also on seed traits. Seed traits, such as seed size, seed coat thickness, seed mass, and seed shape, are important to determine seed survival in the gut passage and survival for germination (Bruun and Poschlod, 2006; Kleyheeg et al., 2018). Ideally, small seed size, hard seed coat, low seed mass and round seed shape; experience shorter seed retention time within the gut passage (Picard et al., 2015), boosting germination probability post-gastric (Pakeman et al., 2002; Mouissie et al., 2005b). Seed coat scarification depends on seed traits (Traveset and Verdú, 2002) – larger seeds and those with extremely thin permeable coats

more susceptible to gastric juices (Kleyheeg et al., 2018), and digestive tract gastric level its retention time (Traveset et al., 2001). Germination may also be influenced by differences by seeds age, with mature seeds germinating faster (Prataviera et al., 2015) and frugivores species type (Baltzinger et al., 2019).

1.4 Ungulate species as seed dispersal agents

Avian species are extensively researched concerning their seed dispersal services for fleshy-fruited plant species (Murray, 1988; Traveset et al., 2001; Levey et al., 2005; Jordaan et al., 2011b; Thabethe et al., 2015a; Gioria and Pyšek, 2017; Bitani et al., 2020). In contrast, mammalian species such as ungulates are underestimated but effective seed vectors (Milton and Dean, 2001; Picard and Baltzinger, 2012; Picard et al., 2016), not only of fleshy fruits but of diverse seed types ranging from podded seeds of woody plant species (Coe and Coe, 1987; Miller and Coe, 1993; Miller 1994a, 1994b, 1996), to seeds of leguminous, gramineous and herbaceous plant species (Gardener et al., 1993; Shiponeni and Milton, 2006; Slater and du Toit, 2002; Picard et al., 2015). Significant research on ungulate species as effective endozoochoric dispersers has shown that their gut passage physiology accelerates seed germination (Gardener et al., 1993; Malo et al., 2000; Cosyns et al., 2005a, 2005b; Mouisse et al., 2005; Bartuszevige and Endress, 2008; Picard et al., 2015). This is facilitated by the positive correlation between body size and gut retention time (Demment and van Soest, 1985). The correlation elucidates that larger ungulate species have a longer seed retention time (Illius and Gordon, 1992). The effects on endozoochoric dispersal by the gut passage of ungulates may differ between ruminants and non-ruminants, affecting seed retention time and the degree of seed damage (Clauss et al., 2009, 2011). With the addition of a grazer or browser feeding strategy, potentially, there come more variations in seed germination responses (Demment and van

Soest, 1985). According to Dugger et al. (2018), an increase in body mass and degree of frugivory at the species level is closely associated with an increasing diversity of plant partners. Therefore, the large gut food-intake capacity of ungulate species is advantageous for bulk seed dispersal, transporting large quantities of seeds at a given time (Janzen, 1984; Will and Tackenberg, 2008; Sridhara et al., 2016). A trait-based meta-analysis of 52 studies by Albert et al. (2015) showed that ungulates could disperse up to 44% of plant species within their habitat. Therefore, they are ecologically significant for large-scale intercommunity plant dispersal contributing to plant species richness and abundance (Malo et al., 2000). Similarly, their large body size correlates to a large home range, an important component of ungulate habitat-use and dispersal (du Toit, 1990; Nathan et al., 2008; Picard and Baltzinger, 2012; Picard et al., 2015), essential for transporting and dispersing seeds within their home range (Pellerin et al., 2016; Baltzinger et al., 2019). Therefore, their movement patterns are essential for ecosystem function and influence plant communities' demographics (Pellerin et al., 2016). Conclusively, ungulates are advantageously unique from other seed vectors and potentially more effective in seed dispersal. However, ungulate species' contribution to seed dispersal of fleshy-fruited invasive plant species remains relatively limited in literature; therefore, research is required to understand their influence on plant invasion better.

1.5 Alien invasive plants in South Africa

Ecosystems in South Africa are one of the richest globally, with diverse fauna and flora across varied habitats (Perera et al., 2011), however extensively compromised by alien plant invasions (Wilson et al., 2017; Bennett and Sittert, 2019). Alien invasive plant species have been introduced into South Africa for various reasons, including medicinal purposes, horticulture, agriculture, ornamental purposes (Byrne et al., 2017; Faulkner et al., 2020; Zengeya and Wilson, 2020). Most

initially introduced alien plants were largely intentional (Faulkner et al., 2020). However, a substantial number of invasive plant taxa have been accidentally introduced, and some have dispersed unaided from neighbouring countries (Hulme et al., 2008; Faulkner et al. 2016; Faulkner et al. 2020; Zengeya and Wilson, 2020). Post-introductions, alien plant species are dispersing within the country through various pathways, including human-mediated and through natural processes, such as by rivers and animal-mediated, and multiple pathways (Foxcroft et al., 2019).

The South African legislative system, regulated by the National Environmental Management Biodiversity Act, Act 10 of 2004 (NEM:BA, Act 10 of 2004), has put in place some control measures to manage some of these pathways; however, introductions of alien plants continue at an increasing rate (Faulkner et al., 2020). To date, it has been reported that of the 8750 alien plant species introduced into South Africa, 660 have become naturalised, and 200 are declared as alien invasive plant species (Wilson et al., 2013). However, the number of introduced plant taxa is on the rise (Zengeya and Wilson, 2020). About 7% of the country is estimated to be invaded by alien plants (Moran et al., 2013; van Wilgen, 2018), thus severely suffering from ecological, economic and societal impacts incurred by alien plant species (Davies et al., 2016; van Wilgen, 2018; Wilson et al., 2017). Therefore, thus far, invasions of alien species in South Africa are responsible for a quarter of biodiversity loss (van Wilgen et al., 2008), and South Africa is one of the countries leading globally in the severity of alien plant invasions (Richardson and van Wilgen, 2004; Wilson et al., 2017). Additionally, governmental organisations have been developed for alien plant management (McConnachie et al., 2012) and biodiversity conservation (van Wilgen and Wannenburgh, 2016; Bennett and Sittert, 2019). Working for Water (WfW), the largest national conservation body, was established in 1995 by the South African government (van Wilgen et al., 1998; Richardson and van Wilgen, 2004), mainly targeting riparian zones (Holmes et al.,

2005; van Wilgen and Wannenburgh, 2016). Through the WfW programme, over 500 million USD has been devoted to managing alien invasive plant species (van Wilgen and Wannenburgh, 2016; Bennett and Sittert, 2019). However, most invasive plant species are controlled by chemical and mechanical methods (van Wilgen et al., 1998; Richardson and van Wilgen, 2004) but have proven ineffective. Nevertheless, the effectiveness of invasive alien plant species has been observed for biological control (Zengeya and Wilson, 2020). Most recently, in the financial year of 2018/2019, more than 1000 million ZAR was spent by the Department of Forestry, Fisheries, and the Environment (DFFtE) through the Natural Resource Management programmes on biological invasions in South Africa (Zengeya and Wilson, 2020).

South Africa is one of the top five countries with significant advancements in alien plant biological control research (van Wilgen et al., 2004; Moran et al., 2013), involving native range surveys and host specificity testing (Day et al., 2020). Biological control has been used to combat an array of alien plant species from aquatic to various forms of terrestrial species in South African since the early 20th century (Zimmermann et al. 2004). *Opuntia monacantha* is the first alien invasive plant to be effectively controlled using a biological agent (cochineal insect, *Dactylopius ceylonicus*) in South Africa, as early as 1913 (Klein, 2011; Zimmermann, 2010; Paterson et al., 2011), providing cost-effective control of this invasive plant. Due to a variety of control initiatives, the South African government has generated an estimation of 6.6 billion USD in ecosystem service restoration revenue because of alien invasive plant control (Stafford et al., 2017). However, the effort required to manage all plant invasions surpasses the available resources (Kaplan et al., 2017), as the persistence of alien plant invasions remains an economic concern in South Africa (Bhagwat et al., 2012). Concerns have arisen about the programme's cost-effectiveness (Moran et al., 2013; van Wilgen, 2009) and whether the management and eradication methods are long-term effective

(McConnachie et al., 2012; van Wilgen et al., 2012). Although the South African government has employed laws and conservation bodies, the problem of alien plant invasion has not decreased (van Wilgen, 2018). Moreover, management programmes target well-established invasive plants, yet attention should also be given to emerging alien plants to control and eradicate at their initial emergence stage (Nel et al., 2004). Though some biocontrol agents become established against their targeted invasive plants, their long-term control has been insignificant. In the case of experiencing long-term impacts from plant invasions, regulatory and management response, and biocontrol research, South Africa is an exemplary global model for alien invasion control (van Wilgen et al. 2020b). However, the mechanisms associated with the transport of and spreading of seeds of alien invasive plants are poorly studied, especially in savannahs which play an important role in human livelihoods. Thus, the spread of alien invasive plants in these savannahs is likely to threaten human livelihoods (Zengeya and Wilson, 2020). To provide additional information on other dispersal pathways of alien invasive plant species, a comprehensive understanding of the dispersal pathways of alien plant invasion processes leading to the continuous spread of alien plants is important for effective management.

1.6 Problem statement

The spread of alien invasive plants via seed dispersal (Richardson and van Wilgen, 2004) incurs major detrimental impacts on the biodiversity of native ecosystems (Yemshanov et al., 2019). Alien plants modify native plant communities, decreasing native habitat availability and negatively affecting native species (Ruwanza and Shackleton, 2016; Ramaswami et al., 2016; Nkambule et al., 2017). Fleshy-fruited alien invasive plants provide frugivorous species with a nutritional reward from the fruit pulp (Jordaan and Downs, 2012b). Frugivorous species, in turn, provide a

seed dispersal service (Baltzinger et al., 2019). Therefore, fleshy-fruited invasive alien plants form part of native dispersal networks (Early et al., 2016; Ramaswami et al., 2016; Martin-Albarracin et al., 2018). Although African ecosystems are rich in ungulate species diversity and habitat richness (du Toit and Cumming, 1999; Holmes et al., 2005; Perera et al., 2011), they are highly invaded by alien invasive plants (Wilson et al., 2017; Bennett and Sittert, 2019). However, the contribution of ungulate species to seed dispersal, including their role in the spread of alien invasive plants, is poorly documented in this region. The majority of studies on seed dispersal of fleshy-fruited alien invasive plants in South Africa have concentrated on their seed-frugivore dispersal interactions with avian species for seed germination purposes (Jordaan et al., 2011a; Thabethe et al., 2015b; Dlamini et al., 2018), with relatively little literature focussed on ungulate species (Milton and Dean, 2001; Slater and du Toit, 2002). Therefore, information regarding the seed-frugivore dispersal interactions of ungulate species with fleshy-fruited alien invasive plants is limited, despite their importance in facilitating plant invasion of fleshy-fruited invasive species.

1.7 Aims and objectives

The overall aim of this study was to obtain an understanding of the seed dispersal relationship and role of wild southern African ungulates with fleshy-fruited invasive lantana (*L. camara*), bugweed (*S. mauritianum*), syringa (*M. azedarach*) and cochineal prickly-pear (*O. monacantha*), on Fountainhill Estate, Zingela and Nkonka Lodge-Nyala Pans, KwaZulu-Natal, South Africa. Our main objectives were to:

- (1) Determine visitation and fruit consumption of alien invasive plants by potential wild southern African ungulates;

- (2) Determine the role of ungulate species as seed predators or seed dispersers of alien invasive plants via faecal content analyses; and
- (3) Determine potential seed dispersal distances of alien invasive plants by wild southern African ungulates.

It was predicted that: (1) a community of wild southern African ungulates would visit and ingest the fleshy-fruits of the alien invasive plants; (2) the role of ungulate species would vary, some would act as dispersers and others as predators; and (3) potential seed dispersal distances (km) and mean retention times (h) of wild southern African ungulates would vary among ungulate species, directionally associated with body mass (kg) and variations in home range size (km²) and daily travelled distances (km).

1.8 Study sites

The present study was conducted on three private game properties in the province of KwaZulu-Natal (KZN), South Africa: Fountainhill Estate, Zingela Safari and Water Company (Zingela) and Nkonka Lodge - Nyala Pans (NLNP) (Fig. 1.1). All sites are in the south-east part of South Africa, receiving summer rainfall (November – January) and dry winters (June – August). Although all the sites experience similar seasonality conditions, they are vegetatively unique from one another. The first site, Fountainhill Estate (ca. 2330-ha; 29°27'34.72" S, 30°32'43.55" E) is a multi-purpose land-use in Wartburg, composed of a 1600-ha conserved nature reserve and a 730-ha commercial farm of sugarcane (*Saccharum officinarum*) and avocado (*Persea americana*). It experiences a minimum and maximum mean annual temperature range of 3.3 °C to 37.4 °C, respectively, with a mean annual precipitation of 805 mm (Musokwa et al., 2019). The site is characterised by a Sub-Escarpment Grassland biome of a Dry Coast Hinterland Grassland vegetation type, and a Sub-

Escarpment Savannah biome of the KZN Hinterland Thornveld, the KZN Sandstone Sourveld, and a small patch of the Eastern Valley Bushveld vegetation types (Mucina et al. 2018). The Dry Coast Hinterland Grassland is of sparse sourveld grassland plains with wooded undulating sloping valleys. The KZN Hinterland Thornveld is a typical savannah-like habitat, with open thornveld dominated by acacia *Vachellia* plant species at river valleys' margins. The KZN Sandstone Sourveld is species-rich, predominately short grassland with scattered short shrubs on steep slopes with plateauing hilltops (Mucina and Rutherford, 2011)

The second site, Zingela (28°43'01.67" S, 30°03'47.74" E), forms part of a mosaic habitat of a protected and conserved reserve, semi-protected private game reserve and unprotected communal areas of free-ranging wildlife and livestock, on the outskirts of Weenen and Colenso, KZN. Data from the present study were sampled from the semi-protected private game reserve, predominately inhabited by free-ranging wildlife. The site is found in a Sub-Escarpment Savannah biome, comprised of the Thukela Valley Bushveld and the Thukela Thornveld vegetation types (Mucina et al. 2018). The Thukela Valley Bushveld is rocky sloped, highly eroded with shallow soils, and predominately ground-covered by the endemic succulent plant species of *Euphorbia pseudocactus* and *Blepharis natalensis*, with deciduous trees, such as acacia *Vachellia* species. The Thukela Thornveld is acacia *Vachellia* dominated, with wooded grassland of impenetrable thickets and dense grassy ground layer (Mucina and Rutherford, 2011).

Lastly, Nkonka Lodge (ca. 3000-ha; 30°00'05.91" S, 30°11'12.20" E) and Nyala Pans (ca. 3000-ha; 29°59'27.96" S, 30°09'46.80" E), are adjacent to one another, located in the valleys of Umkomaas River, KZN. Free-ranging wildlife and livestock are rotated between these two sites, therefore subsequently considered as one large area for this study, namely Nkonka Lodge - Nyala Pans (29°59'43.84"S, 30°11'062"E) (NLNP). The site is comprised of the Sub-Escarpment

Savannah biome of the Eastern Valley Bushveld vegetation type (Mucina et al. 2018), characterised by a mosaic of semi-deciduous savannah woodlands and thickets (Mucina and Rutherford, 2011).

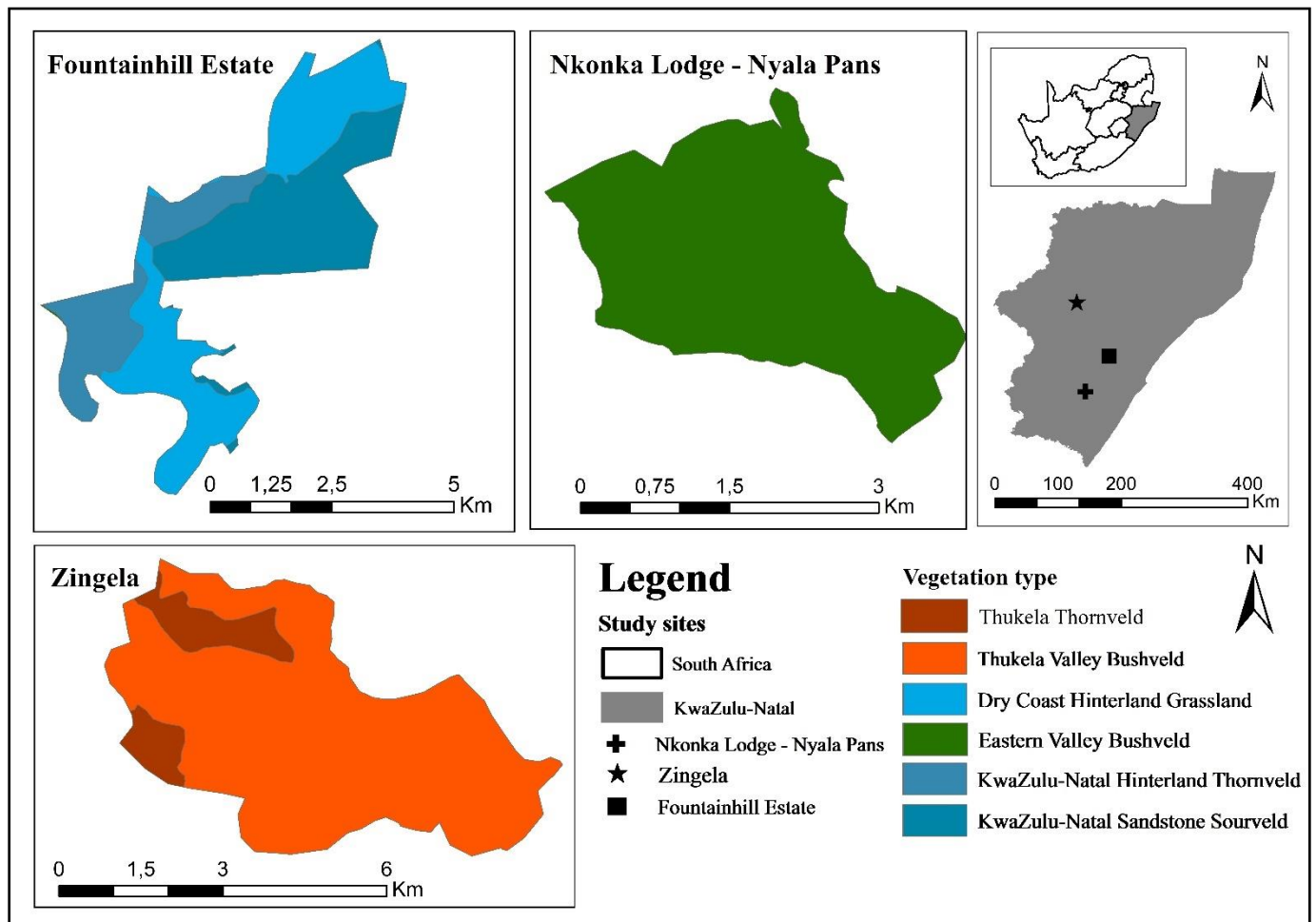


Figure 1.1. Study sites showing vegetation types of Thukela Thornveld, Thukela Valley Bushveld, Dry Coast Hinterland Grassland, Eastern Valley Bushveld, KwaZulu-Natal Hinterland Thornveld and KwaZulu-Natal Sandstone Sourveld within the Sub-Escarpment Grassland and Sub-Escarpment Savannah biome in KwaZulu-Natal, South Africa.

1.9 Study species

1.9.1 *Lantana camara*

Lantana camara is an aggressive invasive weed (Baars and Neser, 1999; Vardien et al., 2012; Fig. 1.2a), originating from South and Central America (Henderson, 2001; Ruwanza and Mhlongo, 2020). In South Africa, it was initially introduced in the 1850s as an ornamental and hedge plant in the Western Cape, and then in KwaZulu-Natal in the 1880s (Wells and Stirton, 1988; Urban et al., 2011). It has now been estimated to have invaded approximately 2 million-ha country-wide (Shackleton et al., 2017). Its allelopathic chemical emission interferes with plant regeneration (van Wilgen et al., 2001; Bhagwat et al., 2012), causing a decrease in relative abundance and biodiversity of natural ecosystems, and reducing grazing palatability of pastures (van Wilgen et al., 2008; Shackleton et al., 2017). Of the 650 varieties of *L. camara*, approximately 50 varieties are found in South Africa, therefore making control and manage difficult (Bromilow, 2010; Vardien et al., 2012), even though 21 different biocontrol agents have been released against this invasive shrub (Zimmermann et al. 2004). The whole plant and unripe fruits are poisonous to both humans and livestock (Henderson, 2001), causing organ failure and sometimes eventually death (Shackleton et al., 2017). However, avian species were suggested to be the main vectors of *L. camara* in South Africa (Jordaan et al., 2011a). This has been followed by an assemblage of 38 avian species observed ingesting and dispersing *L. camara* (Bitani and Downs, *in prep.*). The invasive shrub grows up to 2m and sometimes higher (Jordaan et al., 2011a; Bitani et al., 2020; Fig. 1.2a), and fruits all year round (Henderson, 2001). On average each shrub annually produces 856 small single-seeded fleshy fruits that have a mean fruit size of 4 mm (Jordaan et al., 2011a; Bitani et al., 2020; Fig. 1.2b). Though the rate of seed germination is low, seeds that have been ingested by avian species shows a trend of an increased germination post-gastric (Jordaan et al., 2011a).

Nonetheless, the interactions of frugivores with *L. camara* is poorly documented, and the invasive degree and distribution of *L. camara* cannot be explained only by dispersal of avian species. Therefore, additional research is required to understand dispersal patterns of *L. camara* by additional vectors to determine suitable management practices.

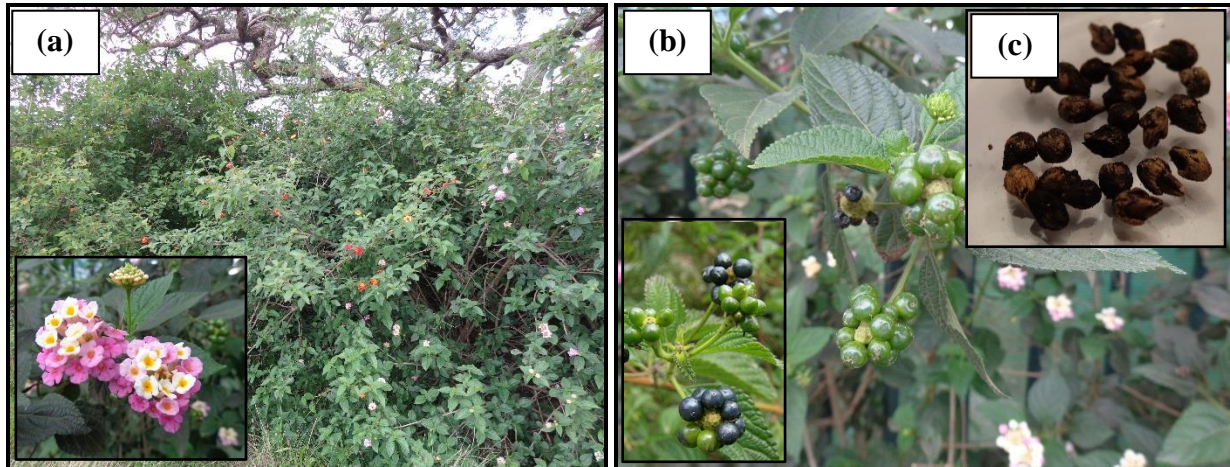


Figure 1.2. Photographic images of *Lantana camara* infestation with multi-coloured flowers (a), green unripe and purple-black ripe fruits (b), and seeds (c).

1.9.2 *Solanum mauritianum*

Solanum mauritianum is an evergreen invasive shrub (Olckers, 1998; Olckers, 1999; Fig. 1.3a); native to Argentina, Brazil, Uruguay, and Paraguay (Cowie et al., 2018). It was accidentally introduced globally during the 16th Century by a ship of the Portuguese trade routes (Olckers, 2011); therefore, becoming problematic in Australia, Madagascar, New Zealand and South Africa (Singh and Olckers, 2017). It was first recorded in KwaZulu-Natal, South Africa, in the 1860s, as an ornamental plant (Singh and Olckers, 2017). It has been estimated to have invaded approximately 80 500-ha (Cowie et al., 2018), but mainly flourishing in higher rainfall regions of South Africa (Olckers, 1998). It is a transformer species, thus converts the structure of plant

communities by outcompeting native plant species (Olckers, 2011). Moreover, its fast-growing nature shades out surrounding vegetation (Bromilow, 2010; Cowie et al., 2018). Mechanical, chemical and biological management options are used to control *S. mauritianum*, but copious seed production and high seed survival in seed banks promote an aggressive return post-management (Campbell and van Staden, 1983; Goodall et al., 2017). South Africa is the only country with two released biocontrol agents against *S. mauritianum* (Olckers, 2011; Cowie et al., 2018), with New Zealand only recently implementing a biocontrol programme (Singh and Olckers, 2017). Although many biocontrol experiments have been conducted to combat invasive plants such as *S. mauritianum* (Olckers, 2011), none have been entirely effective and invasive shrubs remains highly problematic. Unripe fruits of *S. mauritianum* are toxic (Henderson, 2001; Cowie et al., 2018). However, ripe fruits serve as food sources for frugivorous avian species (Jordaan et al., 2011a). A dietary shift by native frugivorous avian species with a preference for (Witkowski and Garner, 2008) and inclusion of *S. mauritianum* more than native fleshy-fruited plant species have been observed (Mokotjomela et al., 2013), potentially dispersing the invasive shrub. In addition to avian species, mammalian species such as bats (Olckers, 2011; Jordaan et al., 2011a) and potentially ungulates may serve as seed vectors of *S. mauritianum*. The invasive tree grows between 2-10 m and sometimes higher (Henderson, 2001; Singh and Olckers, 2017), mainly fruiting from September to March, and sometimes until June, with some reports of fruiting all-year-round (Goodall et al., 2017). On average, annual seed production ranges between 100,000-20,000 seeds/plant (Olckers, 2011; Singh and Olckers, 2017) of fruits with a mean fruit size of 13.7 mm (Thabethe et al., 2015b; Bitani et al., 2020). Much consideration has been given to the germination of *S. mauritianum* after ingestion by avian species (Campbell and van Staden, 1983; Jordaan et al., 2011a; Thabethe et al., 2015b), which has shown high germination seed viability

patterns (Campbell and van Staden, 1983; Witkowski and Garner, 2008). However, these are influenced by seasonality and seed age (Campbell et al., 1992; Goodall et al., 2017). Nevertheless, research is required on the influences of seed dispersal by mammalian species such as ungulate species.

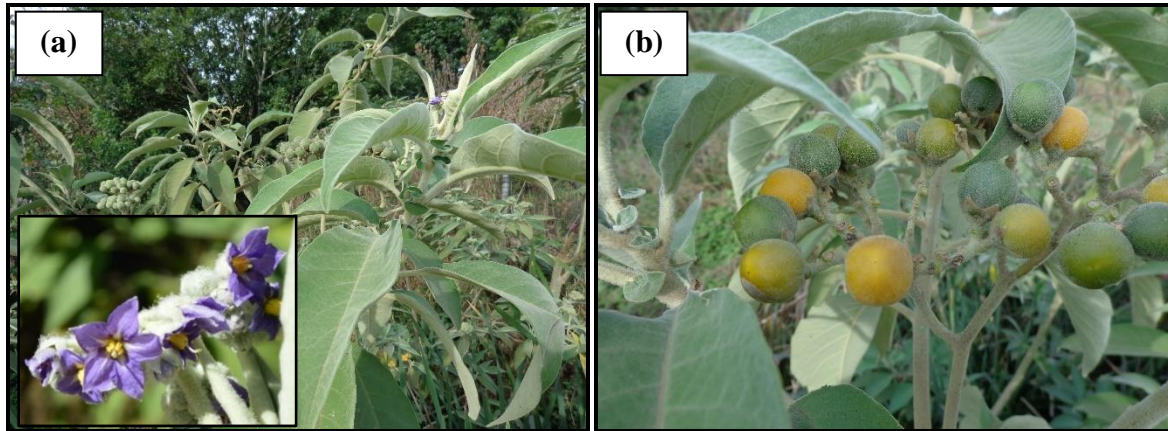


Figure 1.3. Photographic images of *Solanum mauritianum* with self-compatible purple-lilac flowers (a), and green unripe and yellow ripe fruits (b).

1.9.3 *Melia azedarach*

Melia azedarach (syringa) is an invasive deciduous tree (Botha and Penrith, 2009; Voigt et al., 2011; Fig. 1.4a), originating from southern Asia to northern Australia (Tourn et al., 1999; Tilney et al., 2018). Within the native range, the South African cultivar is native to India (Voigt et al., 2011). In South Africa, it was introduced for ornamental purposes (Henderson, 2001; Stavarache et al., 2008) and first recorded in Cape Town in the 1800s (Voigt et al., 2011). It has highly invaded the margins of forests, roadsides and riparian zones (Holmes et al., 2005; Voigt et al., 2011), especially in the savannah biome (Tilney et al., 2018). Due to the invasion, native ecosystems have been transformed by converting the structure of plant communities (Henderson, 2001). Although

M. azedarach have a relatively short lateral root system, their tap root is sent deep underground for water (Tourn et al., 1999), therefore possibly outcompeting indigenous plants for water resources. Moreover, the invasive tree is highly defensive against insects and pathogens, therefore, more advantageous than native plant species (Stavarache et al., 2008). All parts of the plant are poisonous (Ntalli et al., 2010; Lungu et al., 2011), especially the fruits (Stavarache et al., 2008). The toxicity of fruits is influenced by environmental variables, with some trees not being toxic at all (Botha and Penrith, 2009). The invasive tree grows between 12 m (Corlett, 2005; Bitani et al., 2020) and up to 23 m (Henderson, 2001), and fruits during the dry season in South Africa (Voigt et al., 2011). The single-seeded fleshy drupes are characterized by a mean fruit size of 11.9 mm (Corlett, 2005; Bitani et al., 2020; Fig. 1.4d; Fig. 1.4c). Fruit bats (Jordaan et al., 2011b) and avian species largely source the ripe fruits for food (Wirminghaus et al., 2002; Voigt et al., 2011). Therefore, further investigation and understanding of the seed dispersal pathways of *M. azedarach* are important for effective management strategies.

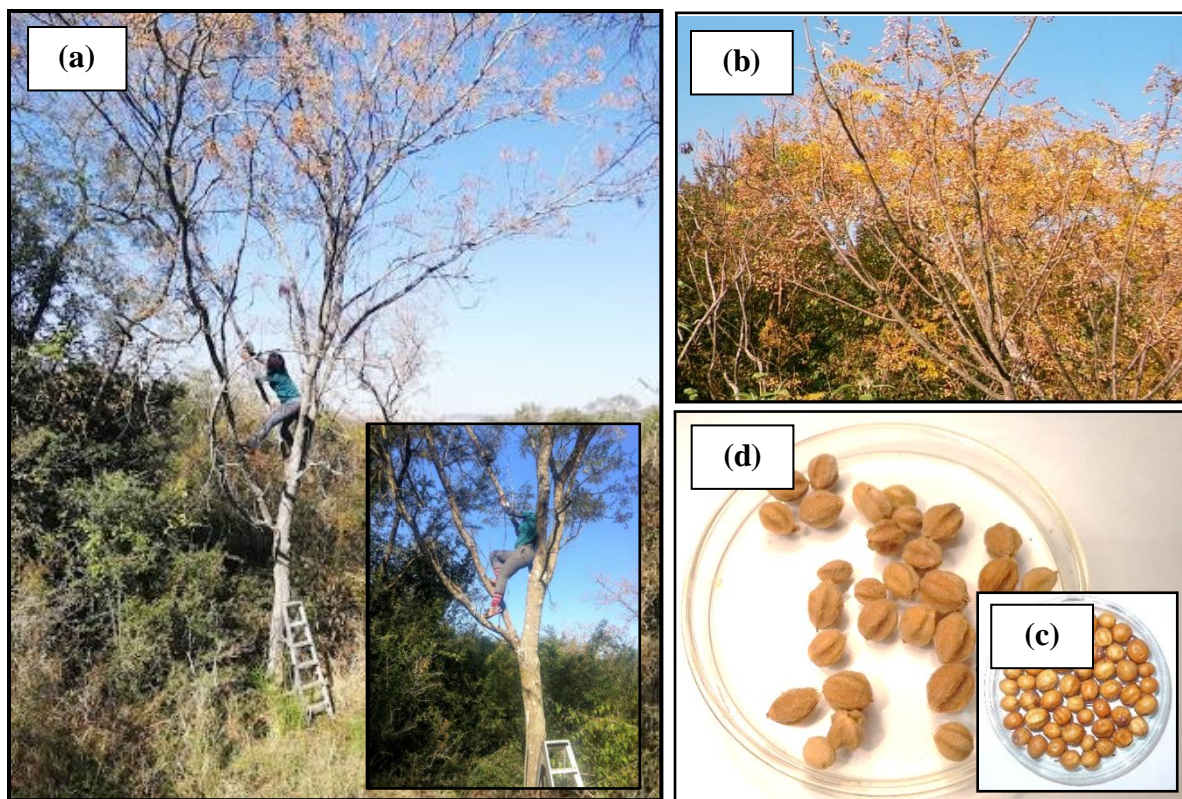


Figure 1.4. Photographic images of a mature *Melia azedarach* fruiting trees (a, b), yellowish-brown ripe fruits (c), and seeds (d).

1.9.4 *Opuntia monacantha*

Opuntia monacantha (cochineal or drooping prickly pear), previously *Opuntia vulgaris* (Klein, 2011), is a thorny succulent invasive shrub (Bromilow, 2010; Fig. 1.5a). It originates from South America, particularly Brazil, northern Argentina (Henderson, 2001), Paraguay and Uruguay (Valente et al., 2010). It has become naturalised in Cuba, China, India, the Himalayas, Australia and South Africa (Valente et al., 2010). By the 1770s, the succulent invasive shrub was already present in South Africa (Klein, 2011) and declared problematic by the 1980s (Zimmermann et al., 2004). It was introduced for dye production from cochineal insects (*Dactylopius* spp.) (Faulkner et al., 2020) and as a security hedge (Henderson, 2001; Kaplan et al., 2017). In South Africa, it has

threatened indigenous diversity (Wells et al., 1986) by invading agricultural rangelands in the savannah biome (Bromilow 2010). This has resulted in the degrading of rangelands by reducing grazing pasture accessibility (Thrash, 1998) and promoting livestock injury because of their large spines, subsequently reducing livestock productivity (Kaplan et al., 2017). The invasive shrub grows up to 5m, producing egg-shaped fleshy fruits of 60 mm in size, with copious seeds (Henderson, 2001; Fig. 1.5b; Fig. 1.c). The invasive succulent shrub spreads via vegetative budding, promoting the rapid spread and dense infestation (Zimmermann, 2010). Moreover, it spreads via seed dispersal by frugivorous avian and mammalian species (Thrash, 1998). However, the literature lacks species assemblage of these frugivores.

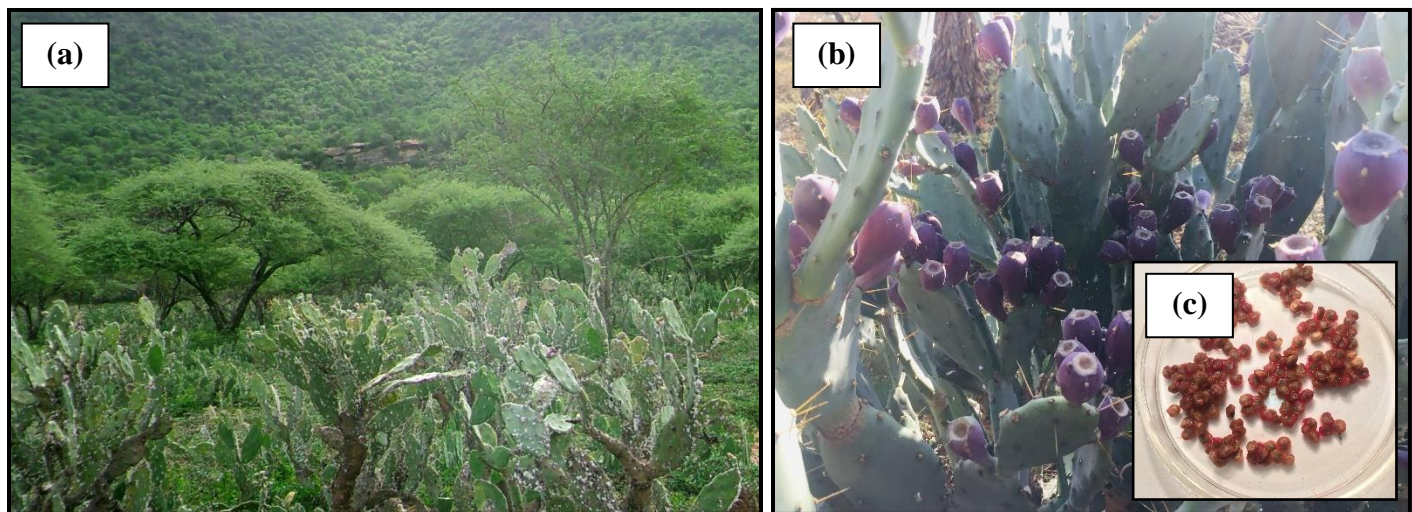


Figure 1.5. Photographic imagery of infestation of fruiting *Opuntia monacantha* (a, b), ripe purple fruits (b), and seeds (c).

1.10 Structure of the thesis

The main body of this thesis is organised as manuscripts prepared for publication in peer-reviewed journal articles. The first chapter (Chapter 1) is the Introduction which provides the literature

review of the concepts covered in this study. The next three data chapters (Chapter 2, 3 and 4) are experimental chapters with each one covering a specific objective. Each chapter is formatted according to the peer-reviewed journal it is intended to be (or has been) submitted. Because of this thesis format, a certain degree of repetition, especially in the methods section, was unavoidable. However, this is deemed to be of little concern as this format allows the reader to read each chapter separately without losing the overall context of the thesis. In Chapter 2, we investigated wild southern African ungulate species visiting and ingesting the seeds of fleshy-fruited invasive lantana (*L. camara*), bugweed (*S. mauritianum*), syringa (*M. azedarach*) and cochineal prickly pear (*O. monacantha*). Chapter 3 investigated whether wild southern African ungulates are seed predators or seed dispersers of fleshy-fruited invasive alien plants by analysing their faecal content. In Chapter 4, we estimated mean retention times and dispersal distances of wild southern African ungulates that ingested, and seeds of alien invasive plants found in their faecal droppings. Lastly, Chapter 5 is the conclusion chapter, where the main findings of the study are discussed and summarised, with recommendations.

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CHAPTER 2

To eat or not to eat: visitation and fruit consumption of fleshy-fruited alien invasive plants by wild southern African ungulates

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Running header: Visitation and fruit removal of alien invasive plants by ungulates

2.1 Abstract

Animal visitation and fruit consumption to fruiting plants are fundamental for the process of seed dispersal. Endozoochory seed dispersal by ungulates has received increased attention recently. However, patterns of visitation and ingestion of the fleshy fruits of alien invasive plants by ungulates are poorly documented. Our aim was to document visitation and fruit consumption of freshly-fruited alien invasive *Lantana camara*, *Solanum mauritianum*, *Melia azedarach* and *Opuntia monacantha* by wild southern African ungulates in KwaZulu-Natal, South Africa, using camera-trapping. Our objectives were to: (1) determine the community of potential ungulate seed-dispersers of the invasive plants; and (2) quantify the strength of the interactions with the invasive plants. A total of 1277 images and 162 videos of ungulate frugivory activity were captured. The total number of visitations with fruit consumption (intensity of interactions) and the total number of visitations with and without fruit consumption (frequency of interactions) were used as an estimate of the seed-dispersing role of each ungulate species. We tested for significant differences in visitation and fruit removal frequencies to fruiting invasive plants between different ungulates. Diverse species of ungulates were observed visiting and ingesting the fruits of *L. camara*, *O. monacantha* and *S. mauritianum*, but only ingested the fruits of *L. camara* and *O. monacantha*. No data were captured for both animal visitation and fruit consumption of syringa (*M. azedarach*), because of fruit accessibility because of height constraints. The main ungulates potentially dispersing *L. camara* were giraffe *Giraffa camelopardalis* and bushbuck *Tragelaphus sylvaticus*, and impala *Aepyceros melampus* and greater kudu *Tragelaphus strepsiceros* for *O. monacantha*. There were significant differences in visitation frequencies between ungulates for *L. camara*, *O. monacantha* and *S. mauritianum*. Furthermore, there were significant differences in fruit removal frequencies of *O. monacantha* between different ungulates; however, no significant differences

were observed for *L. camara*. Our study showed that camera-trapping is useful for determining the interactions between ungulates and the alien invasive plants, which is important for understanding their potential contribution to the dispersal dynamics of invasive plant species in African savannahs.

Keywords: Fleshy-fruited alien invasive plants • Camera-trapping • Ungulates • Animal visitation • Fruit consumption • Seed dispersal

2.2 Introduction

Animal-mediated seed dispersal involves animal dispersal interaction with the plant species whose seeds are to be dispersed (Janzen 1984; Schupp et al. 2017). Of the diverse ways animals disperse seeds, endozoochory is the most popular and well-studied dispersal mechanism (van Leeuwen et al. 2020). Endozoochoric seed dispersal involves complex successional processes undertaken by the seeds: from animal visitation and fruit consumption (Schupp 1993; Prasad et al. 2010; Campos et al. 2018), seed transportation via the gut of the animal-disperser (Grünewald et al. 2010; Mokotjomela et al. 2013; Picard et al. 2016), to seed deposition at suitable microhabitats for germination of viable seeds (Westcott et al. 2005; Jordaan and Downs 2012a; Kuprewicz 2013; Thabethe et al. 2015a). Collectively, these successional processes potentially lead to seed dispersal (Traveset et al. 2007; Miguel et al. 2018), consequently influencing plant spatial distributions (Cain et al. 1998; Pellerin et al. 2016), plant demography and regeneration (Howe and Smallwood 1982; Baltzinger et al. 2019). Moreover, animal visitation and fruit consumption to fruiting plants are crucial subcomponents in determining the quantitative component of seed dispersal effectiveness (Schupp et al. 2010; Schupp et al. 2017). Both subcomponents elucidate the number

of seeds an animal can disperse at a given time (Vázquez et al. 2005). Thus, animal visitation and fruit consumption are used as strength of interaction factors, estimating the frequency of interactions and intensity of interactions, respectively (Schupp 1993; Campos et al. 2018).

In endozoochoric seed dispersal, frugivorous species show preferences for fruits based on traits, such as fruit type, fruit release height, fruit palatability and nutritional content (Janzen 1984; Gosper and Vivian-Smith 2009, 2010; Jordaan and Downs 2012a, 2012b; Jordano 2014; Thabethe et al. 2015a), which influences the probability of fruit-animal frugivory interaction (Picard et al. 2015). Moreover, according to Sridhara et al. (2016), large herbivorous mammals possess the same taste cues as humans (salty, sweet, umami, sour, and bitter); therefore, similar fruit selection patterns between large herbivores and humans may be observed. In light of this, a mutualistic relationship exists between fleshy-fruited plants and animal-dispersers with a nutritional reward from fruit pulp for frugivores and dispersal service by frugivores for the plant (Bodmer 1991; Wilson and Downs 2012; Zungu and Downs 2017). Given that globally, the majority of plant species in many ecosystem types, particularly in tropical and sub-tropical regions, are characterised by fleshy fruits (Howe and Smallwood 1982; Wilson and Downs 2012), suitable for large mammalian ingestion and dispersal (Donatti et al. 2007), there is an expectation of a plethora of research exploring frugivory interaction of fleshy fruits with large mammalian species.

Although some studies have investigated ungulates species as seed vectors (Milton and Dean 2001; Slater and du Toit 2002; Shiponeni and Milton 2006; Picard and Baltzinger 2012; Picard et al. 2015; Pellerin et al. 2016), the interaction of fleshy fruits with ungulate species are rarely investigated. In theory, herbivorous mammals such as ungulates choose their habitat of occupancy and plant species to interact with based on food availability (Smuts 1975; Picard et al. 2016) and landscape structure (Breitbach et al. 2012; Zungu et al. 2020). However, the invasion

of alien plants has altered some of these interactions (Baltzinger et al. 2019), allowing for interactions of ungulates with invasive plants (Miller and Coe 1993; Milton and Dean 2001; Slater and du Toit 2002; Shiponeni and Milton 2006), potentially contributing to their invasion. Alien invasive plants are non-native plants species that negatively impact ecosystems and biodiversity, triggering a decline in native habitat availability (Traveset and Richardson 2006; Bitani et al. 2020), influencing native plant species distribution, richness and abundance (Gaertner et al. 2009; Vilá et al. 2011). They proliferate and spread via seed-dispersers (Traveset and Richardson 2006; Bitani et al. 2020) transporting their seeds to expand their population distribution. Particularly in African savannahs, literature has shown potential dispersal of woody alien invasive plants, i.e. *Vachellia* species (Miller and Coe 1993; Miller 1996), and alien grass species (Shiponeni and Milton 2006). However, the role of ungulates as seed dispersal agents of fleshy-fruited alien invasive plants is poorly documented.

The quantitative component of seed dispersal effectiveness of frugivorous species is effectively studied using direct focal observations, as all subcomponents required are accounted for; however, these favour arboreal frugivore observations (Prasad et al. 2010; Rivas-Romero and Soto-Shoender 2015). Consequently, camera-traps have been used as a non-invasive technique to monitor endozoochory frugivory interactions of ungulates species (Prasad et al., 2010; Bridges and Noss, 2011; Campos et al., 2016; Campos et al., 2018). Camera-trapping is a valuable technique for monitoring mammalian processes such as animal visitation and fruit consumption (Prasad et al. 2010; Campos et al. 2018), habitat occupancy and daily activity patterns (Ramesh and Downs 2015; Ehlers Smith et al. 2018; Zungu et al. 2020). When studying large herbivorous mammals, such as ungulates, camera-traps are useful for accurate animal species identification and nocturnal activity detection (Rivas-Romero and Soto-Shoender 2015). Therefore, to quantify

quantitative component of seed dispersal effectiveness (SDE), camera-traps are suitable for deriving information for assessing ungulate frugivory activities.

Our aim was to document the strength of the interactions (frequency of interactions and intensity of interactions) between southern African ungulate species with the alien invasive *Lantana camara*, bugweed *Solanum mauritianum*, syringa *Melia azedarach*, and cochineal prickly-pear *Opuntia monacantha*. Our main objectives were to (1) determine the community of potential ungulate seed-dispersers of the invasive plants, and (2) quantify and compare their strength of interactions with ungulates. We hypothesised that (1) a diversity/wide range of wild southern African ungulate species would ingest fruits of alien invasive plants, and (2) strength of interactions between the invasive plants and ungulate species would vary depending on the invasive plant.

2.3 Methods

2.3.1 Study area

Our study was conducted on three private game properties in KwaZulu-Natal Province, South Africa: Fountainhill Estate (FHE), Zingela Safari and Water Company (Zingela) and Nkonka Lodge–Nyala Pans (NLNP) (Fig. 2.1). All the sites are located in the south-east of South Africa, which receives summer rainfall, with January being the wettest month and June the driest month. A diversity of 16 ungulate species occurs across the three study sites; 15 species in FHE, 11 species in Zingela, and nine species in NLNP (Supplementary information Table S2.1). FHE (ca. 2330-ha; 29°29'34.25"S, 30°30'55.97"E) is a multi-purpose land-use habitat comprised of a 1600 ha conserved nature reserve and a 730-ha commercial farm. It experiences a mean annual minimum and maximum temperature of 3.3 °C and 37.4 °C, respectively, with a mean annual precipitation

of 805 mm (Musokwa et al. 2019). The study site comprises of a Dry Coast Hinterland Grassland, the KZN Hinterland Thornveld, the KZN Sandstone Sourveld, and a very small patch of the Eastern Valley Bushveld vegetation types (Mucina and Rutherford 2011; Mucina et al. 2018). Zingela (28°43'24.74"S, 30°03'55.80"E) forms part of a mosaic habitat of protected, semi-protected and unprotected communal areas with free-ranging wildlife in the outskirts of Weenen and Colenso. The study site comprises of the Eastern Valley Bushveld vegetation type (Mucina and Rutherford 2011; Mucina et al. 2018) and has extreme soil erosion (pers. obs.). Nkonka Lodge (ca. 3000-ha; 30°00'05.91"S, 30°11'12.20"E) and Nyala Pans (ca. 3000-ha; 29°59'27.96"S, 30°09'46.80"E) are adjacent to another, both practising free-ranging game and cattle, in the Umkomaas River Valley. Game and cattle move freely, rotating between these two sites. Therefore, the two sites were considered as one large area for this study, namely Nkonka Lodge–Nyala Pans (29°59'43.84"S, 30°11'062"E) (NLNP), because they are experiencing the same practice and management. The site comprises of Thukela Valley Bushveld and Thukela Thornveld vegetation types (Mucina and Rutherford 2011; Mucina et al. 2018).

2.3.2 Study species

Lantana camara is an aggressive invasive (Baars and Neser 1999; Vardien et al. 2012), originating from tropical America (Ruwanza and Mhlongo 2020). In South Africa, it was initially introduced in the Western Cape in the 1850s (Bromilow 2010), then in KwaZulu-Natal in the 1880s (Urban et al. 2011); introduced as an ornamental and hedge plant (Henderson 2001), and later used for mulching (Vardien et al., 2012) and leaves sourced for medicinal use (Maema et al. 2019). It is now estimated to have invaded 2 million ha (Shackleton et al. 2017). In South Africa, it is declared a category 1b invasive species, meaning that it forms part of an invasive species control

programme; therefore, management and control are compulsory (National Environmental Management: Biodiversity Act, Act 10 of 2004) (NEM:BA, Act 10 of 2004). It has invaded degraded habitats of native forest and plantation margins, pastures, and river-banks (Baars and Naser 1999) reducing native species diversity (Ruwanza and Mhlongo 2020). It grows up to 2 m and sometimes higher (Henderson 2001; Bitani et al. 2020), flowering from September to April, and some cultivars flowering and fruiting year-round (Henderson 2001). The small single-seeded fleshy fruits form drupes and are shiny green when unripe but turn dark purplish-black when ripe (Henderson 2001), with a mean fruit size of 4 mm (Jordaan et al. 2011a; Bitani et al. 2020). Although avian species are suggested to be the main vectors of *L. camara* (Jordaan et al. 2011a; Bitani and Downs, *in prep.*), additional research is required to understand dispersal patterns of *L. camara* by additional vectors. In our research sites, *L. camara* is densely populated, forming thicket clusters within savannah and thicket habitats in FHE and NLNP, but sparsely distributed in Zingela (pers. obs.). It is partially managed through chemical control in FHE and Zingela, and no management initiatives have been undertaken in NLNP.

Solanum mauritianum is a fast-growing evergreen invasive weed (Henderson 2001; Olckers 2011) native to South America (Henderson 2001). It was first recorded in KwaZulu-Natal, South Africa, in the 1860s as an ornamental plant (Olckers and Hulley 1991) and is now estimated to have invaded 80 500 ha (Cowie et al. 2018). It grows between 2-10 m and sometimes higher (Henderson 2001), producing fruits year-round (Goodall et al. 2017). The fleshy fruits with copious seeds (Cowie et al. 2018) are green when unripe but turn dull yellow when ripe (Olckers 2011) and have a mean fruit size of 13.7 mm (Jordaan et al. 2011a; Thabethe et al. 2015b; Bitani et al. 2020). In South Africa, it is also declared under category 1b (NEM:BA, Act 10 of 2004), invading indigenous forest and timber plantations (Goodall et al. 2017), agricultural lands and

along riverine zones (Singh and Olckers 2017), therefore, out-competing surrounding vegetation (Cowie et al. 2018). In our research sites, *S. mauritianum* is sparsely distributed across all three sites (pers. obs.) and not managed or controlled in all the study sites.

Melia azedarach is an invasive deciduous tree (Tourn et al. 1999; Voigt et al. 2011), originating from southern Asia to northern Australia (Tourn et al. 1999). However, the South African cultivar is native to India (Voigt et al. 2011). In South Africa, it was first recorded in Cape Town in the 1800s (Voigt et al. 2011) as an ornamental plant and for shade provision (Henderson 2001). It grows up to 12 m (Bitani et al. 2020) and sometimes up to 23 m (Henderson 2001), flowering between September and November (Henderson 2011). The single-seeded fleshy drupes are green when unripe but turn yellowish-brown when ripe (Botha and Penrith 2009), with a mean fruit size of 11.9 mm (Corlett 2005; Bitani et al. 2020). In South Africa, it is also declared under category 1b (NEM:BA, Act 10 of 2004) and has highly invaded disturbed habitats of forest margins and along river courses and roadsides (Henderson 2001; Voigt et al. 2011). Although the invasive plant has a relatively short lateral root system (Tourn et al. 1999), the taproot pierces deep underground for water, therefore likely outcompeting indigenous plants for water resources. In our research sites, *M. azedarach* is relatively sparsely distributed across all three sites along rivers and mostly found along riverbanks (pers. obs.).

Opuntia monacantha is a thorny succulent shrub (Bromilow 2010), originating from South America, particularly in Brazil and northern Argentina (Day et al. 2020). In South Africa, it was introduced for dye production from the cochineal insects (*Dactylopius* spp.) (Faulkner et al. 2020) and as a security hedge (Henderson 2001). It grows up to 5 m, flowering from October to April. The egg-shaped fleshy fruits are edible, with small spikes, green when unripe but turn reddish-purple when ripe and have a fruit size of 60 mm (Henderson 2001). In South Africa, it is also

declared under category 1b (NEM:BA, Act 10 of 2004), invading degraded areas of agricultural rangelands and savannah biomes (Bromilow 2010). In our research sites, *O. monacantha* only occurs in Zingela, in severely eroded soils, and the largest population is found in degraded woodland habitat (pers. obs.).

2.3.3 Camera-trapping survey

Animal visitation and fruit consumption observations were conducted simultaneously during the fruiting seasons of *L. camara*, *S. mauritianum*, *M. azedarach*, and *O. monacantha* using camera-trapping. We used simple random sampling to select each camera-trap station, determined by the presence of ripe fruits on the shrubs or trees of AIPs, treating each camera-trap station location as a random observational point. A total of 20 camera-trap (Moultrie M880i, LLC, Alabaster, USA) sites were established, six at FHE (21/05/2018 – 11/06/2018), eight at NLNP (18/07/2019 – 20/08/2019), and six at Zingela (26/10/2019 – 16/11/2019) for 21 consecutive days per camera-trap location. We standardised the camera-trap survey across all the study areas for consistency; however, we set some for photographic images and others for video recording. Before the commencement of the camera-trap installation, we conducted a field assessment survey to select camera-trap stations of areas invaded by the invasive plants, through direct observations done by driving and walking active wildlife trial transects. Although the camera-trap stations within the infested areas were not placed using a systematic grid, each camera-trap station selected was guided by an inter-trap distance of 200 m or more, depending on the size of fruiting stands of the invasive plants collectively. The chosen camera-trap stations were placed viewing and focusing on the fruiting stands of the invasive plants near active wildlife trails, guided by the presence of ungulate dung signifying habitat-use by ungulates in that sampling area. Camera-traps were

installed approximately 1-3 m away from the fruiting invasive plants, and between 2-6 m in height to accommodate for the varying heights of ungulate species present in the area.

2.3.4 Data analyses

We examined all images and videos captured by the camera-traps, and independent animal visitation events of individuals were considered using the procedures described in Rivas-Romero and Soto-Shoender (2015) and Campos et al. (2018). The number of fruits consumed could not be quantified with the trap camera; therefore, the total number of fruits consumed by the ungulates was substituted and recorded as the total number of visitations with fruit consumption (the act of seed ingestion observed in the photographs and videos). The numbers of visitations with fruit consumption by ungulates to the fruiting alien invasive plants were considered as an estimate of the intensity of interactions; and total numbers of independent animal visits (with or without fruit consumption) were considered as the frequency of interactions (Schupp 1993; Campos et al. 2018). We compared both frequencies of interactions and intensity of interactions between ungulate species for each invasive plant using Chi-square tests to determine significant differences in their patterns between different ungulates. Once the community of ungulate species visiting and ingesting the alien invasive plants was determined, the overall strength of interactions (combining both frequencies of interactions and intensity of interactions) was determined. We conducted all statistical analyses using IBM SPSS Statistics (SPSS Inc, version 27, USA).

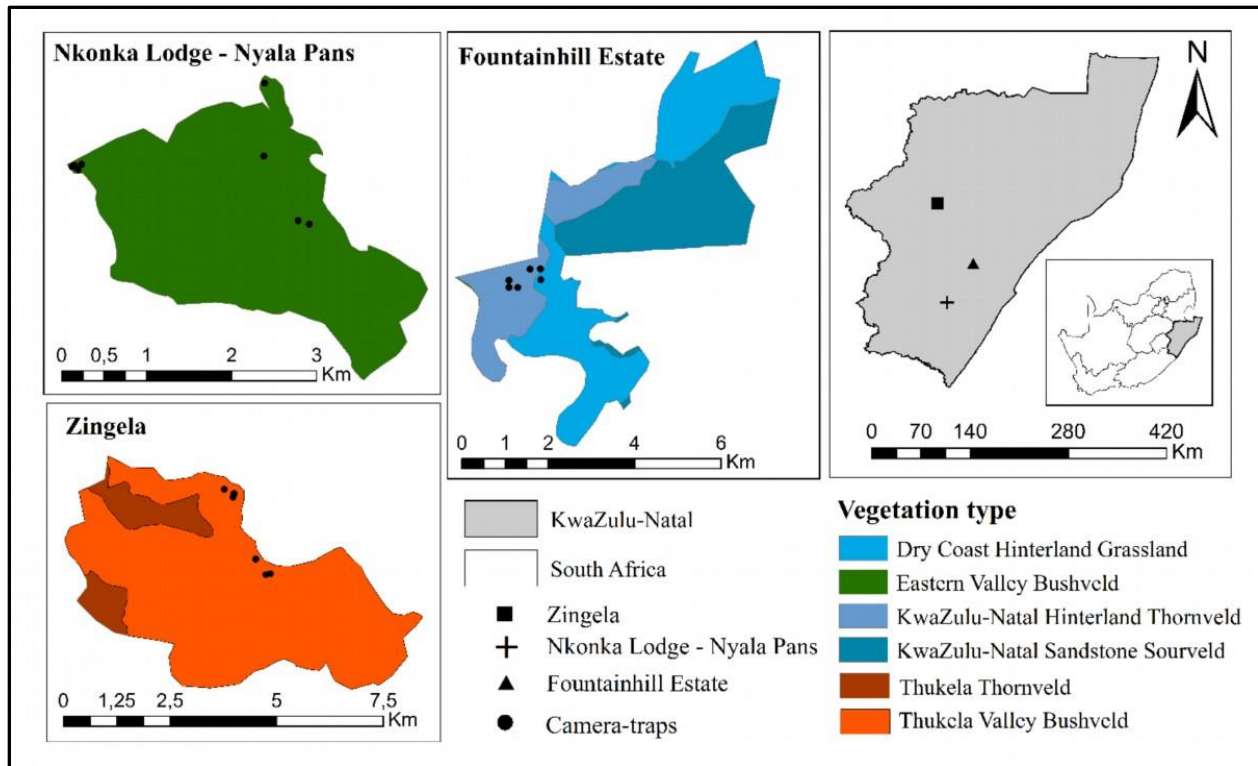


Figure 2.1. Camera-trap placement within vegetation types of the Sub-Escarpment Grassland and Sub-Escarpment Savannah biome in KwaZulu-Natal, South Africa.

2.4 Results

We collected a total of 1277 photographs and 162 videos of independent ungulate activity during the 420 camera-trap nights. Overall, eight ungulate species (giraffe, *Giraffa camelopardalis*; impala, *Aepyceros melampus*; nyala, *Tragelaphus angasii*; zebra, *Equus quagga*; blue wildebeest, *Connochaetes taurinus*; greater kudu, *Tragelaphus strepsiceros*; common warthog, *Phacochoerus africanus*; and bushbuck, *Tragelaphus sylvaticus* were recorded visiting fruiting alien invasive plant species. Of the eight ungulate species, only one species (common warthog) did not show evidence of alien invasive plant fruit consumption throughout the camera-trap survey (Table 2.1; Fig. 2.2). Across the different study sites, we found four ungulate species were observed ingesting alien invasive fruits in FHE, two species in Zingela, and four species in NLNP (Supplementary

information Table S2.1). *Lantana camara* was mostly ingested by giraffe and bushbuck, respectively (Table 2.1, Supplementary information Fig. S2.1). Of the six ungulate species observed visiting *O. monacantha*, only impala and greater kudu showed evidence of fruit consumption (Table 2.1, Fig. 2.2, Supplementary information Fig. S2.1). Overall, both *L. camara* and *O. monacantha* were visited by diverse ungulate species; however, the fruits of *L. camara* were ingested more frequently compared with *O. monacantha*. Therefore, the overall strength of interactions (mean \pm SD) (total visitation frequency and total fruit consumption frequency of ungulate species observed visiting and ingesting the fruits) were as follows impala (99.75 ± 132.510), giraffe (54.20 ± 58.465), greater kudu (37.00 ± 57.050) and bushbuck (29.60 ± 31.699). These ungulate species were observed to have the greatest strength of interaction with alien invasive plants (Table 2.1).

A total of 929 independent animal visitation events were recorded for both total animal visitation (frequency of interactions) (77%, $n = 719$) and animal visitation with fruit consumption (intensity of interactions) (23%, $n = 210$). Frequency of interactions with fruiting *L. camara* by different ungulate species varied significantly ($\chi^2 = 373.013$; $p < 0.0001$; $df = 7$; Table 2.2) however, the intensity of interactions (fruit removal) was not significantly different between ungulate species ($\chi^2 = 3.090$; $p = 0.079$; $df = 1$; Table 2.2). Frequency of interactions and intensity of interactions of *O. monacantha* by different ungulates varied significantly ($\chi^2 = 755.289$; $p < 0.0001$; $df = 5$) and ($\chi^2 = 335.192$; $p < 0.0001$; $df = 1$; Table 2.2), respectively. Frequency of interactions of *S. mauritianum* varied significantly for different ungulate species ($\chi^2 = 101.974$; $p < 0.0001$; $df = 3$; Table 2.2); and intensity of interactions for *S. mauritianum* were not recorded as ungulate species that visited the invasive shrub did not ingest on the fruits (Table 2.2). No data

were captured for both animal visitation and fruit consumption in the camera-traps for *M. azedarach*, owing to tree height constraints and camera-trap placement (Table 2.2).

Table 2.1 Overall strength of interactions (mean \pm SD), total visitation frequency and total fruit consumption frequency of ungulate species observed visiting and ingesting the fruits of *L. camara* (Lc), *O. monacantha* (Om) and *S. mauritianum* (Sm).

Ungulates	Overall strength of interactions (mean \pm SD)	Total visitations			Total fruit consumption	
		Lc	Om	Sm	Lc	Om
Giraffe, <i>Giraffa camelopardalis</i>	54.20 \pm 58.465	138	23	18	92	0
Impala, <i>Aepyceros melampus</i>	99.75 \pm 132.510	64	296	0	18	21
Nyala, <i>Tragelaphus angasii</i>	18.60 \pm 15.241	37	29	7	20	0
Zebra, <i>Equus quagga</i>	1.50 \pm 1.732	3	0	0	3	0
Blue wildebeest, <i>Connochaetes taurinus</i>	6.00 \pm 8.165	4	18	0	2	0
Greater kudu, <i>Tragelaphus strepsiceros</i>	37.00 \pm 57.050	6	122	0	4	18
Common warthog, <i>Phacochoerus africanus</i>	11.00 \pm 10.198	21	11	16	0	0
Bushbuck, <i>Tragelaphus sylvaticus</i>	29.60 \pm 31.699	40	0	76	32	0

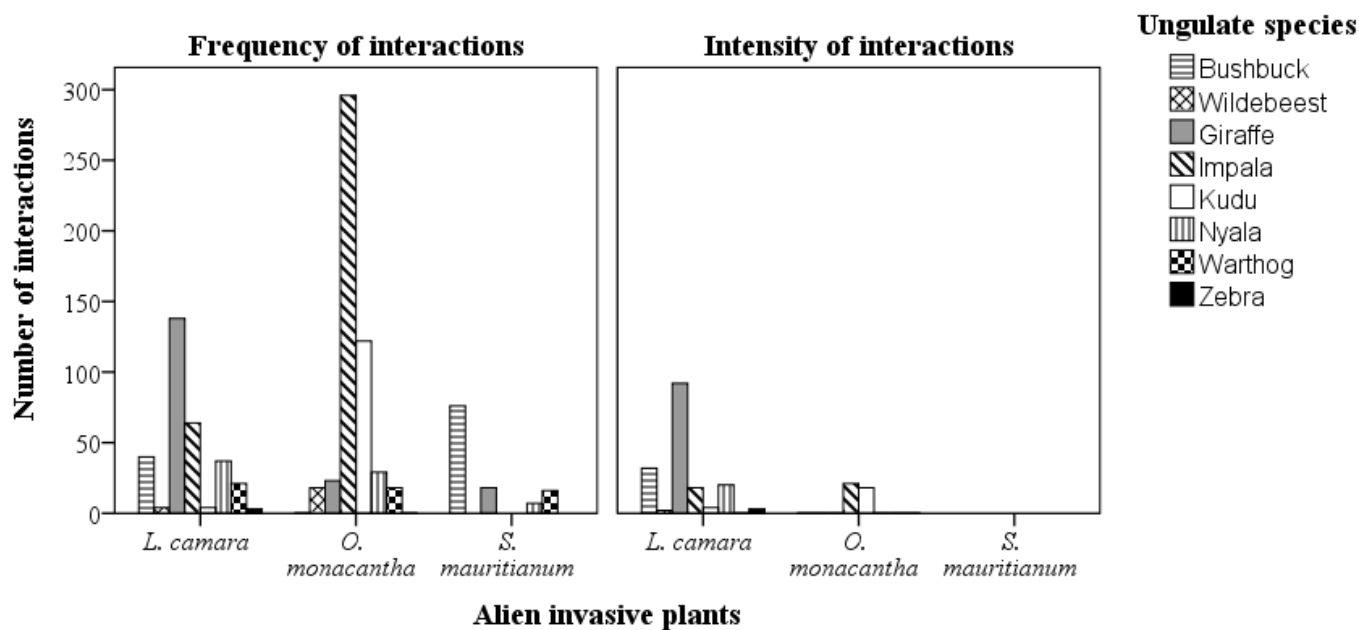


Figure 2.2. Animal visitation (frequency of interactions) and fruit consumption (intensity of interactions) by a guild of ungulate species (Table 2.1) observed interacting with the alien invasive *L. camara*, *O. monacantha* and *S. mauritianum* in the present study.

Table 2.2 Frequency of interactions and intensity of interactions of ungulate species with alien invasive *L. camara*, *O. monacantha* and *S. mauritianum* (NS not significant; S significant).

Alien invasive plants	Frequency of interactions					Intensity of interactions			
	χ^2	p-value	df			χ^2	p-value	df	
<i>L. camara</i>	373.013	< 0.0001	7	S		3.090	0.079	1	NS
<i>O. monacantha</i>	755.289	< 0.0001	5	S		335.192	< 0.0001	1	S
<i>S. mauritianum</i>	101.974	< 0.0001	3	S					

2.5 Discussion

Animal visitation and fruit removal are important to quantitatively determine animal dispersers dispersal efficiency (Schupp 1993; Schupp et al. 2017). In this study, we report on the frequency of interactions and intensity of interactions of wild southern African ungulates on alien invasive plants using camera-trapping. Though precise measurements of the number of fruits ingested could not be estimated because of the nature of the study, camera-trapping showed that diverse ungulate species visit and ingest fruits of fleshy-fruited alien invasive plants. We identified eight ungulate species (giraffe, impala, nyala, zebra, blue wildebeest, greater kudu, common warthog and bushbuck) visiting the fleshy-fruited alien invasive plants. However, only common warthogs did not ingest the fruits during the camera-trap survey. Despite the lack of literature on seed dispersal of fleshy-fruited invasive plants by ungulates, Grünewald et al. (2010) reported on the effectiveness of ungulate visitation and ingestion of fleshy fruits of wild cherry (*Prunus avium* L., Rosaceae) for dispersal purposes. Similarly, Prasad et al. (2010) investigated fruit removal of fleshy-fruited Indian gooseberry (*Phyllanthus emblica*) and discovered that of the two species contributing to a 95% fruit removal, one was Spotted deer (*Axis axis*), an ungulate species. Additionally, the ungulate species had previously regurgitated viable seeds of *P. emblica* that successfully germinated (Prasad et al. 2004, 2006); therefore, solidifying the role of the ungulate species as the primary disperser of the fleshy-fruited *P. emblica*.

There was a significant difference in frequencies of interactions between ungulate species that visited *L. camara*. Giraffe, impala, bushbuck and nyala were observed to have the greatest visitation frequency, respectively. Only bushbuck, giraffe, common warthog and nyala were observed visiting *S. mauritianum*; however, none of the ungulates ingested the fruits of *S. mauritianum*. According to Vázquez et al. (2005), visitation frequency may sometimes be used as

an estimator of fruit removal when fruit removal is difficult to validate. However, in some instances, this is not the case, as some visitors do not consume fruits (Howe 1986), as was observed for common warthogs in this study. Therefore, visitation frequencies could not be used as an estimator of fruit removal, amplifying the importance of differentiating between visitation with fruit consumption and visitation without fruit consumption. The published literature lacks information on the relationship of the studied fleshy-fruited invasive plants with ungulates on fruit consumption and potential dispersal. However, on Fountainhill Estate, an assemblage of 28 avian species was observed visiting and ingesting the fruits of *L. camara*, potentially dispersing the seeds (Bitani and Downs, *in prep.*). In the case of *O. monacantha*, there was a significant difference in frequencies of interactions between ungulate species. Impala and greater kudu had significantly higher visitation frequencies than nyala and giraffe, respectively. Bushbuck and zebra were observed not visiting the fruiting *O. monacantha* during the camera-trap survey. Vázquez et al. (2005) suggested that animal visitation rates may sometimes be influenced by species abundance. Therefore, the frequent interaction of ungulate species with the alien invasive plants is perhaps influenced by species abundance, and this may be the case for extremely high visitation rates for impala. Similarly, the invasive plants had lower interaction rates by less abundant ungulate species, and this may be the case for extremely low visitation and fruit consumption rates for blue wildebeest and zebra.

We expected a lower fruit removal of *L. camara* by ungulates, since the invasive plant is reported to be toxic to ungulates, causing organ failure and eventually death (Henderson 2001; Botha and Penrith 2009; Vardien et al. 2012). Although we found that a guild of ungulate species visited both *L. camara* and *O. monacantha*; the fruits of *L. camara* were more frequently ingested than those of *O. monacantha* despite the high toxicity of *L. camara* (Henderson 2001). It is possible

that over time, ungulates have developed a coping mechanism to deal with the toxicity of *L. camara*. According to Launchbaugh et al. (2001), ungulates develop both innate and learned feeding strategies to cope with toxic chemicals in plant species, eventually tolerating the toxins and ingesting more of the plant.

Moreover, greater fruit ingestion of *L. camara* than *O. monacantha* may have resulted because all three sites (FHE, Zingela, and NLNP) were highly infested by *L. camara*, resulting in a higher number of observations than *O. monacantha*, which only occurred at Zingela in a randomly scattered distribution of smaller population size (pers. obs.). There were no significant differences in the intensity of interactions between ungulate species with *L. camara*; however, giraffes were ingesting the fruits of *L. camara* the most, followed by bushbuck. There were significant differences in the intensity of interactions between ungulate species with *O. monacantha*. This suggests a greater probability that the visitation of ungulate species to *L. camara* resulted in fruit ingestion, and visitation to *O. monacantha* resulted in a much lower probability of fruit ingestion. We expected more ungulates to ingest on *O. monacantha* as their fruits are sweet and ingested by humans as well. These expectations stemmed from the notion of large herbivores that possess similar tastes cues as humans (Sridhara et al. 2016). Moreover, ingestion of *O. monacantha* may have been limited by landscape structure, as most ungulates did not inhabit the areas where the largest *O. monacantha* population was found. This confirmed previous studies showing that ungulates habitat occupancy is determined by food accessibility and landscape structure (Smuts 1975; Zungu et al. 2020). Moreover, in Zingela, impala and greater kudu were frequently observed foraging on *Blepharis natalensis*, a thorny succulent ground-creeper endemic to this region of KwaZulu-Natal (pers. obs.). We also expected higher numbers of fruit removal of *O. monacantha* by giraffe since this ungulate species was also observed feeding on other thorny

succulent plants, of *Aloe* species (pers. obs.). However, our expectations were not met, as giraffe only visited *O. monacantha* but did not ingest the fruits.

Although the camera-traps captured no animal visitation data to *M. azedarach* and fruit removal by ungulate species of *S. mauritianum* and *M. azedarach* because of tree height constraints, we do not entirely conclude that the ungulate species do not interact with these invasive species. Fruit choice by frugivorous species is regulated by fruit accessibility, depending on fruit position on the plant species (Gosper and Vivian-Smith 2009, 2010; Jordano 2014; Thabethe et al. 2015b). Fruit accessibility to ungulates is determined by tree height, which collectively ranges from 2-23 m (*L. camara* the shortest and *M. azedarach* the tallest) for the studied invasive species. Of the ungulate species captured ingesting fruits of the invasive plants, ungulate maximum body height ranges from 0.75 - 6.1 m (impala the shortest and the giraffe the tallest). Therefore, ungulates can only access fruits within their body height, causing fruits beyond their body height more inaccessible, and also depending on how low the branches of taller trees are hanging. In the study sites, both *S. mauritianum* and *M. azedarach* were not chemically and mechanically controlled. Therefore, both invasive plants had grown to a mature stage and reaching their maximum height (per. obs.), so they were not in the height range where all ungulate species could ingest fruits. Moreover, differences in feeding techniques may influence fruit preference, as some ungulates might have fed on fallen fruits of *S. mauritianum* and *M. azedarach*, which were not captured in this study; therefore, a further investigation is needed to verify this claim.

The use of a camera-trap survey for the present study was significant, as the survey operated as a species inventory for animal species generally interacting with the fleshy-fruited alien invasive plants. Therefore, use of camera-traps resulted in by-catch data of animal species not intended for the present study. For *L. camara*, by-catch data included visitation and ingestion

by domestic cattle (*Bos taurus*) and various avian species. However, identification of avian species would be difficult using camera-trapping because of their small body size, therefore support focal observations of the interaction of *L. camara* with avian dispersers as conducted by Bitani and Downs (*in prep.*). By-catch raw data uncovered that *O. monacantha* was heavily ingested by chacma baboons (*Papio ursinus*) during the camera-trap survey. In a study by Slater and du Toit (2002), it was reported that seeds of grasses, forbs and woody plants particularly found in the dung of chacma baboons remained relatively more viable for seed germination than seeds found in the dung of ungulates, suggesting that chacma baboons are likely more effective as dispersers. *Melia azedarach* was also visited and ingested by a primate species, vervet monkeys (*Chlorocebus pygerythrus*) and various avian species. As reported by Voigt et al. (2011), that seven avian species ingest the fruits of *M. azedarach*, and seeds germinate and therefore successfully disperse this invasive tree. Although the raw by-catch data were not analysed for this study, we recommend further interactive explorations of these vertebrate frugivorous species with the fleshy-fruited alien invasive plants to understand their dispersal pathways.

The main aim of our study was to determine ungulate species assemblage that are potentially responsible for dispersing alien invasive plants (*L. camara*, *S. mauritanum*, *M. azedarach* and *O. monacantha*), and to assess their frequency and intensity of interactions. The results suggested that *L. camara* and *O. monacantha* were more potentially dispersed by giraffe and bushbuck; and impala and greater kudu, respectively. The use of camera-trapping enabled the identification of ungulate species visiting and ingesting the alien invasive plants during diurnal and nocturnal plant-animal interactions. However, the number of fruits ingested were not estimated, which is necessary for establishing the seed dispersal effectiveness of each ungulate species. Nonetheless, the results showed that diverse ungulate species visit and ingest the fleshy

fruits of the studied alien invasive plants. To estimate seed dispersal effectiveness, the number of seeds ingested by an ungulate species can be estimated using the total number of bites, approximated from the total number of fruits per bite and the total number of seeds per fruit. With camera-trapping, observations would only be conducted through video recording to note the precise number of bites. Moreover, with intense field observations (focal sampling) as with direct (timed) observations, one can precisely estimate the total number of fruits ingested per unit time, from both fallen fruit ingestion and direct fruit-on-tree ingestion, as well as total visitation time, which can then be used to determine seed dispersal effectiveness, as done in avian studies.

Importantly, the present study expands our knowledge of plant-animal interactions by providing insights on ungulate-alien invasive plant interactions that potentially contribute to seed dispersal of invasive plants. The present study's information collaboratively provides an understanding of wide distributions and high infestation of the alien invasive plants, especially *L. camara*. We understand that fruit consumption alone by the ungulates does not infer that the species indefinitely disperse the alien invasive seeds successfully. We are cognisant that some species may not be effective dispersers, but rather seed predators (Schupp et al. 2010). Therefore, we advise further investigation of wild southern African ungulates' faecal content, to determine if the ungulate species contribute to the seed dispersal or if they are seed predators. We also propose further research that reports on community-wide level frugivorous species responsible for effectively dispersing the seeds of the fleshy-fruited alien invasive plants in the present study, as it is crucial to understand metacommunity plant-frugivore interactions.

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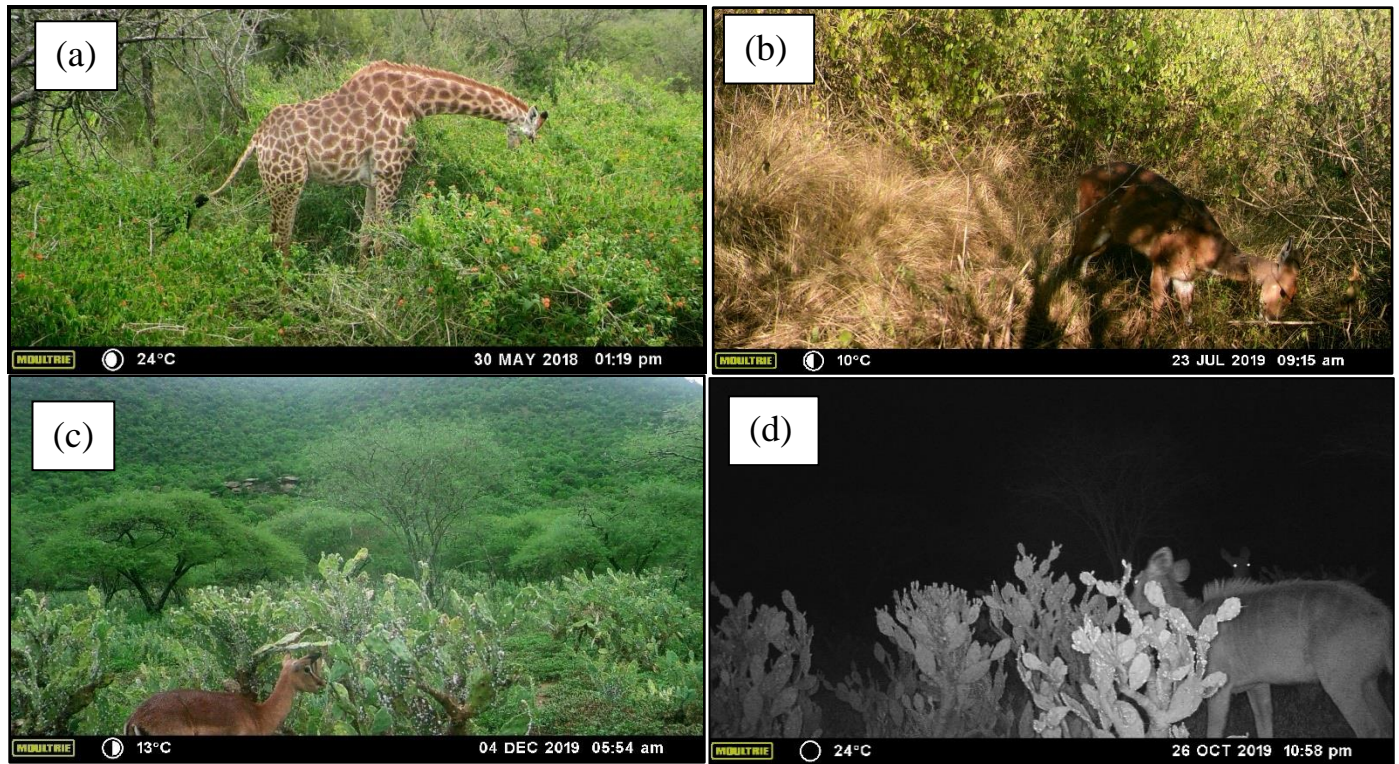
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2.8 Supplementary information

Supplementary information Table S2.1 Wild southern African ungulate species occurring in Fountainhill Estate (FHE), Zingela, and Nkonka Lodge–Nyala Pans (NLNP) in KwaZulu-Natal, South Africa, in the present study (✓ = present, ✗ = not present; Y = ingested fruit, N = did not ingest fruit).

Ungulate species	Feeding type	FHE	Zingela	NLNP
Blesbok, <i>Damaliscus pygargus phillipsi</i>	Roughage grazer	✓ (N)	✗	✗
Blue wildebeest, <i>Connochaetes taurinus</i>	Roughage grazer	✓ (Y)	✓ (N)	✗
Bushbuck, <i>Tragelaphus sylvaticus</i>	Selective concentrate browser	✓ (N)	✓ (N)	✓ (Y)
Bushpig, <i>Potamochoerus larvatus</i>	Roughage grazer	✓ (N)	✓ (N)	✓ (N)
Common duiker, <i>Sylvicapra grimmia</i>	Concentrate browser	✓ (N)	✓ (N)	✓ (Y)
Common warthog, <i>Phacochoerus africanus</i>	Roughage grazer	✓ (N)	✓ (N)	✓ (N)
Eland, <i>Taurotragus oryx</i>	Intermediate mixed feeder	✓*	✓ (N)	✗
Giraffe, <i>Giraffa camelopardalis</i>	Selective concentrate browser	✓ (Y)	✓ (Y)	✓ (Y)
Greater kudu, <i>Tragelaphus strepsiceros</i>	Selective concentrate browser	✓ (N)	✓ (Y)	✓ (Y)
Impala, <i>Aepyceros melampus</i>	Intermediate mixed feeder	✓ (N)	✓ (Y)	✓ (Y)
Mountain reedbuck, <i>Redunca fulvorufula</i>	Roughage grazer	✗	✓ (N)	✗
Nyala, <i>Tragelaphus angasii</i>	Intermediate mixed feeder	✓ (Y)	✓ (N)	✓ (Y)
Red hartebeest, <i>Alcelaphus buselaphus caama</i>	Roughage grazer	✓ (N)	✗	✗
Southern reedbuck, <i>Redunca arundinum</i>	Roughage grazer	✓ (N)	✗	✓ (N)
Waterbuck, <i>Kobus ellipsiprymnus</i>	Roughage grazer	✓ (N)	✗	✗
Zebra, <i>Equus quagga</i>	Roughage grazer	✓ (Y)	✗	✗

* recently introduced in Fountainhill Estate (August 2020), post the camera-trap survey



Supplementary information Fig. S2.1 Camera-trap pictures/snapshots showing *L. camara* (in a, b) and *O. monacantha* (in c, d) being ingested by the four main ungulate species (a: giraffe, b: bushbuck, c: impala, and d: greater kudu) observed having the highest strength of interactions.

CHAPTER 3

Seed composition in the dung of wild southern African ungulates: implications for the dispersal of fleshly-fruited invasive alien plants

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Running header: Dung deposition and seed prevalence in faecal dropping of ungulates

3.1 Abstract

Large herbivorous mammals are keystone species in many terrestrial ecosystems by providing dispersal services to seed-bearing plants. Large mammals' dynamic spatial movement, such as ungulate species across vast habitat types, facilitates seed dispersal. Ungulate species transport seeds in their gut and deposit faecal droppings containing seeds that eventually germinate. Therefore, ungulates are responsible for spatial and temporal patterns of plant species distribution. We conducted a dung deposition survey and a faecal content analysis of seeds in the dung of wild southern African ungulates, in Fountainhill Estate (FHE), Zingela and Nkonka Lodge-Nyala Pans (NLNP), KwaZulu-Natal, South Africa. Our main objectives of the present study were (1) to potentially determine the most vulnerable microhabitat types to plant invasion through dung defecation patterns (number of deposits per ungulate species), and (2) to quantify and compare the prevalence of seeds of fleshy-fruited alien invasive plants. We obtained a total of 2726 dung piles for the depository survey, with varying differences in deposited dung piles among ungulate species and among microhabitats. Dung samples of impala *Aepyceros melampus* and bushbuck *Tragelaphus sylvaticus* were the most common, and common duiker *Sylvicapra grimmia* and zebras *Equus quagga* were the least common. The savannah and grassland microhabitat were found to have the highest dung deposition percentage, and thus are potentially the microhabitats most vulnerable to alien plant invasion. We collected a total of 271 fresh dung piles (54.61 kg, wet mass) during the depository survey. Seed prevalence within faecal droppings varied among ungulate species, habitats, alien invasive plants, and among sites. Overall, we found higher numbers of bugweed *Solanum mauritianum* seeds per dung pile than seeds of lantana *Lantana camara* and prickly-pear *Opuntia monacantha*. No seeds of syringa *Melia azedarach* were found in the dung piles. The dung piles of greater kudu *T. strepsiceros*, bushbuck and nyala *T. angasii*

contained more significant numbers of seeds per dung pile, respectively, while we recorded the lowest number of seeds per dung pile of common warthog *Phacochoerus africanus* and common duiker *Sylvicapra grimmia*. No seeds of fleshy-fruited invasive plants were found in the dung piles of zebra *Equus quagga*. Savannah and thicket microhabitat received the highest number of seed deposition per dung pile. Seed deposition per dung pile varied among sites, with Zingela and NLNP receiving the highest seed deposition per dung piles. High dung deposition and seeds per dung piles in the savannah potentially makes the microhabitat the most vulnerable to alien plant invasion. We recommend a seed deposition survey over consecutive sampling periods to determine temporal and spatial variations in seed deposition of alien invasive plants. Importantly, our study provided foundational information for predicting habitats prone to alien plant invasion, which is important for proactive planning and management of alien invasive plants.

Keywords: Frugivorous ungulates • Fleshy-fruited alien invasive plants • Seed dispersal • Faecal content • Dung deposition

3.2 Introduction

Seed ingestion into frugivore's gut (endozoochory) is critical for seed dispersal. Seed dispersal, the transportation of seeds away from the parent-plant using adaptive dispersal mechanisms to colonize different habitats (Willson and Traveset, 2000; Pakeman, 2001), facilitates plant population establishment and regeneration in plant communities (Minor et al., 2009). Janzen (1984) postulated the 'foliage-is-the-fruit' hypothesis suggesting that large herbivorous mammals potentially dispersing seeds while browsing or grazing on their foliage. Although relatively less documented than avian species, large herbivorous mammals such as ungulates, have been

documented as effective seed dispersers (Couvreur et al., 2005; Shiponeni and Milton, 2006; Picard et al., 2015), significantly important for the maintenance and regulation of plant communities (Pakeman et al., 2002; Couvreur et al., 2005; Mouissie et al., 2005). Moreover, trait-based characteristics of ungulates, in particular their large food-intake capacity, is beneficial for bulk seed dispersal of a variety of plant species at a given time (Will and Tackenberg, 2008; Picard et al., 2016). A trait-based meta-analysis by Albert et al. (2015) showed that ungulates can disperse up to 44% of plant species in each habitat, thus contributing to plant species richness and abundance (Malo et al., 2000). Therefore, the spatial distribution of certain plant species (Malo and Suárez, 1995a, 1995b; Milton and Dean, 2001; Albert et al., 2015) and the modification of plant species composition in habitats are highly accredited to ungulate species (Malo and Suárez, 1995a, 1995b; Malo et al., 2000).

Habitat occupancy by large herbivores is predominately determined by plant composition (Smuts, 1975; Ofstad et al., 2016). Habitat occupancy can be measured by detecting the presence of species in a particular habitat. Indirect methods of assessing species distribution and abundance have been widely used, especially dung deposition of large herbivores (Welch, 1982; Putman, 1984; Jenkins and Manly, 2008). During dung depositions surveys, seeds have been observed germinating directly from defecated faecal dropping of herbivores (Malo and Suarez, 1995a, 1995b), higher dung deposition rates have been observed in open microhabitats (Malo and Suarez, 2000), and higher germination patterns are associated with open microhabitats (Brodie et al. 2009). Therefore, dung depositions are responsible for temporal patterns of plant species (Malo and Suarez, 1995a, 1995b), depending on seed composition of faecal content. Essentially, seed deposition patterns transpire from the interactive relationship between plant species distribution and frugivore behaviour, both varying temporally and spatially (Côrtes and Uriarte, 2013).

Monitoring and examining the faecal content of frugivorous species gives insight into their frugivory dietary composition, giving an indication of their plant-animal interactions (Wrench, 1997). In cases where direct observations of plant-animal frugivory interactions are limited by constraining factors, faecal content analysis, a non-invasive method allowing to sample any number of animals under entirely natural conditions, is an additional technique to explore (Putman et al., 1991; Steward and Steward, 1970). Qualitative dietary research by Cosyns et al. (2005) showed that 117 leguminous and gramineous plant species occurred in the faecal material of ungulate species. Because of longer retention times exhibited by large herbivores, seeds can be defecated over several days, therefore producing a scattered distribution of seed deposition patterns, which is beneficial for seedling recruitment (O'Connor and Kelly, 2012; Sridhara et al., 2016), provided the deposition site is suitable for germination (Traveset, 1998; Traveset and Verdú, 2002; Traveset et al., 2007).

Understanding habitats in ecosystems compromised by alien invasive plant species provides useful information for future conservation purposes. The presence of alien invasive plants in indigenous plant communities threatens biodiversity (Richardson and Wilgen, 2004) by infiltrating, proliferating, and transforming ecosystems (Traveset and Richardson, 2006). Invasive plants form mutualistic relationships with frugivorous species (Voigt et al., 2011), becoming a food source (Buckley et al., 2006). Thus, they form part of indigenous seed dispersal networks (Voigt et al., 2011), potentially spreading and increasing infestations and expanding their distributions (Corlett, 2009). Habitats mostly preferred by frugivorous species receive the largest proportion of viable seeds after defecation (Wenny, 2001; D'hondt et al., 2012). However, with the ingestion and dispersal of invasive alien plants, these preferable habitats become vulnerable to

alien plant invasion (Cosyns et al., 2005). Moreover, defecated seeds persist in seed banks, resulting in high survival rates and invasion capacity (Thompson et al., 1993).

Dung counts of ungulates are extensively studied to estimate relative density, abundance, and patterns of habitat use of ungulate species (Keeping, 2014; Ferretti et al., 2016; Smith, 2016). However, relatively few studies have been conducted to determine the effect of dung deposition patterns by ungulates on seed dispersal spatial patterns. Presently, information is lacking on the spatial dung patterns of southern African ungulates in relation to the dispersal of fleshy-fruited alien invasive plants. Hence little is known about the influence of dung deposition patterns of southern African ungulates on the distribution of fleshy-fruited alien invasive plants.

In southern Africa, initially ungulate species were overlooked as potential dispersers of fleshy-fruited alien invasive plants because of fatalities induced post-ingestion by domestic ungulates (Baars and Naser, 1999; Henderson, 2001; Olckers, 2011). Therefore, few studies have shown the association of southern African ungulates with alien invasive plants (Miller and Coe, 1993; Shiponeni and Milton, 2006; Slater and du Toit, 2002). Most of these studies were conducted on dry-podded fruit type of woody acacia *Vachellia* species (Coe and Coe, 1987; Miller, 1994, 1996), gramineous and herbaceous plant species (Shiponeni and Milton, 2006; Slater and du Toit, 2002). An exception is a study conducted by Milton and Dean (2001), who reported seeds of fleshy fruits in faecal droppings of ungulates. Alien invasive plants tend to fruit all-year-round or fruit in winter (Henderson, 2001) when indigenous plants are low in quantity and quality, becoming available as foliage to frugivores (Ramaswami et al., 2016; Martin-Albarracin et al., 2018). Since ungulates evidently ingest and disperse invasive plants (Milton and Dean, 2001; Myers et al., 2004; Bartuszevige and Endress, 2008), extensive research is required to explore the response on seed composition fleshy-fruited invasive plants in their faecal content and their habitat occupancy based

on dung deposition to deduce most vulnerable habitats. Specifically, an inversely proportional relationship between energy requirements and body size results in smaller herbivores relying on a high energy diet, predominately fruit-based (Demment and van Soest, 1985; Clauss et al., 2003). Therefore, small ruminating herbivores consume more fruits than larger ruminating species (Jarmen, 1974; Clauss et al., 2003). Therefore, larger herbivore diet requirement predominately includes low-quality roughage and browse (Clauss et al., 2013).

Currently, there is a lack of evidence on the importance of southern African ungulates on endozoochoric seed dispersal. The consequence of any fruit-animal frugivory interaction is determined whether the seed vectors play the role of being a seed disperser or a seed predator (Brodie et al., 2009) can be potentially validated by assessing deposition of dung to particular habitats and examining faecal content for seeds (Brodie et al., 2009; Sridhara et al., 2016). Consequently, there is little knowledge about the role of southern African ungulates in invasion biology and their interaction with fleshy-fruited invasive plants. In this study, we examined the contributions of southern African ungulates on endozoochoric seed dispersal of fleshy-fruited lantana (*Lantana camara*), bugweed (*Solanum mauritianum*), syringa (*Melia azedarach*), and cochineal prickly-pear (*Opuntia monacantha*). The role of ungulate species was considered through an analysis of seed composition of their faecal content. We also conducted a dung deposition survey to potentially predict habitats most likely of being invaded by the alien plant species. The purpose of our study was to determine spatial dung patterns of southern African ungulates to predict habitats most vulnerable to alien plant invasion. The main objectives of the present study were: (1) to quantify and compare seed occurrence of the fleshy-fruited alien invasive plants from fresh excreta of wild southern African ungulates; (2) to assess spatial patterns of ungulate dung deposition in microhabitats based on dung counts. We predicted that (1) seed

composition of fleshy-fruited invasive plants would vary in the dung piles of wild southern African ungulates; and that (2) variations in dung deposition would also be detected for the ungulate species.

3.3 Methods

3.3.1 Study area

Faecal samples (ungulate dung piles) were collected in KwaZulu-Natal (KZN) Province, South Africa in three sites: Nkonka Lodge - Nyala Pans (ca. 6000-ha 29°59'43.84"S, 30°11'062"E), Fountainhill Estate (ca. 2330-ha; 29°27'34.72" S, 30°32'43.55" E), and Zingela (28°43'01.67" S, 30°03'47.74" E) (Fig. 3.1). The sites receive summer rainfall from November to January and experience dry winters from June to August. Though similar in seasonality conditions, vegetation composition in each site is unique. Nkonka Lodge - Nyala Pans (NLNP) is a private game lodge practising a mixture of free-ranging wild ungulates and domestic cattle livestock. According to the recent vegetation maps by Mucina et al. (2018), the site is found within the Sub-Escarpment Savannah biome, containing the Eastern Valley Bushveld vegetation type. It is characterised by a mosaic of semi-deciduous savannah woodlands and thickets (Mucina and Rutherford, 2011). Fountainhill Estate (ca. 2330-ha; 29°27'34.72" S, 30°32'43.55" E) is composed of a 1600-ha conserved nature reserve and a 730-ha commercial farm of sugarcane (*Saccharum officinarum*) and avocado (*Persea americana*). The site is found within a Sub-Escarpment Grassland biome and a Sub-Escarpment Savannah biome, therefore containing a variety of vegetation types (Mucina et al., 2018). The Sub-Escarpment Grassland biome is comprised of the Dry Coast Hinterland Grassland, characterized by sparse sour grassland plains with wooded undulating sloping valleys. The Sub-Escarpment Savannah biome is comprised of the KZN Hinterland Thornveld, a typical

savannah-like habitat, with open thornveld dominated by acacia *Vachellia* species at the margins of river valleys; the KZN Sandstone Sourveld, a species-rich vegetation type of predominately short grassland with scattered short shrubs on steep slopes with plateauing hilltops; and a small patch of the Eastern Valley Bushveld (Mucina and Rutherford, 2011). Lastly, Zingela is semi-protected private game reserve of free-ranging wild ungulates, on the outskirts of Weenen and Colenso, KZN. The site is found within a Sub-Escarpment Savannah biome (Mucina et al., 2018), comprised of the Thukela Valley Bushveld vegetation type, characterised by highly eroded rocky slopes with shallow soils, and predominately ground-covered by the endemic succulent plant species of *Euphorbia pseudocactus* and *Blepharis natalensis*, with deciduous trees, such as acacia *Vachellia* plant species. Additionally, it contains the Thukela Thornveld, an acacia *Vachellia* dominated vegetation type, with wooded grassland of impenetrable thickets and dense grassy ground layer (Mucina and Rutherford, 2011). All sites are invaded by alien invasive plants; however, among the sites, *O. monacantha* is only found in Zingela. Moreover, invasion by the alien plants is at different intensities (pers. obs.) as some sites experience alien invasive plant control (FHE) and others do not (NLNP and Zingela).

3.3.2 Dung depository survey

The dung deposition survey was conducted in May, July and October 2019 and June, July and August 2020, to determine dung deposition patterns and habitat occupancy by ungulate species. We conducted the surveys opportunistically using a random sampling where random transect walks along active wildlife trails were performed covering a wide range of microhabitat types (grassland, savannah, thicket, woodland, and degraded woodland). Microhabitats were described according to Kleynhans et al. (2011) and Mucina and Rutherford (2011) (Supplementary

information Table S3.1). The degraded woodland microhabitat is essentially equivalent to the woodland microhabitat. However, the degraded woodland was highly eroded and invaded by *O. monacantha*, for this reason separately classified. During each transect walk, we recorded the geographical location of the deposited dung pile using a Global Positioning System (GPS) (Montana 650, Garmin), the ungulate species to which the dung pile belonged to, and the microhabitat type in which the dung pile was located (grassland, savannah, thicket, woodland, and degraded woodland). To avoid omitting dung samples, a 4-m buffer zone (2-m on each side of the transect) was used to include dung samples on either side of the transect line, as some ungulates do not follow trails. For our study, each dung pile was considered as a separate event, independent of other dung piles of the same species in close proximity. Overall, dung count percentage was used to determine potentially vulnerable habitats based on deposited dung frequency.

3.3.3 Data collection procedure

Tracking sympatric ungulates using dung piles and hoof markings is particularly difficult; therefore, a pilot study was conducted, accompanied by a dung identification expert for a crash course. Thereafter, identifications were made using book guides showing images, size and shape comparisons (Walker, 1986; Stuart and Stuart, 1994, 2000; Cillé, 2000; Murray, 2011). Furthermore, the book guides shared possible misidentifications of similar pellets/piles and how to resolve these misidentifications (Stuart and Stuart, 1994, 2000). We also used samples that were correctly identified by the experts during the crash course as cross-referencing samples. The surrounding dung deposition location was scrutinised to aid in the overall dung identification, thereby developing a step-by-step identification method. Firstly, ungulate hoof markings near the dung piles were identified: to assist in the identification of the dung sample itself. Secondly, the

nature of the defecated dung pile (i.e. clumped, midden or scattered) was deduced to narrow the possible species. Lastly, a fraction of pellets from the dung pile were identified using shape and size, as some dung piles looked identical but varied in individual pellet size. The greatest factor that made dung identification slightly unproblematic was that ungulate species occurring in each study site were known before the study commenced, therefore narrowing the species spectrum of possible dung samples to be found. However, we acknowledge that the process of identifying individual pellets can be difficult, especially for sympatric ungulate species (Hibert et al., 2008). Though dung collection is inexpensive because dung piles are readily available (Wrench, 1997; Smith, 2016), dung processing for seed harvesting is time-consuming. Therefore, focusing only on four invasive plant species for this study eased the processing stage. Faecal decay is problematic when conducting a dung deposition survey (Jenkins and Manly, 2008), therefore potentially obscuring the correlation of dung piles with habitat occupation. For this reason, decaying dung piles were not considered as it was difficult to identify (Hibert et al., 2008; Smith, 2016).

3.3.4 Seed extraction from faecal samples

Fresh dung piles were opportunistically collected simultaneously during the dung deposition survey. Before selecting a dung pile to be collected, we targeted fresh dung samples that were ‘recently defecated’. We achieved this by selecting those that were: not scorched and dried up by the sun, soft-to-touch, and in some cases still warm-to-touch and had the presence of small flying insects (indicating freshness). Fresh dung piles with the presence of beetles were not considered because of the possibility of seed predation by beetles before collection. Dung samples were collected in clear plastic bags, labelled, and weighed (wet mass, in kg) in the field, and stored at the University of KwaZulu-Natal, Pietermaritzburg in a freezer (-17 °C) until dissected for seed

extraction. Dung weight was not controlled to fully report on seed prevalence without excluding a certain portion of the sample. Therefore, the lowermost part of the dung samples was left behind and not collected to avoid contamination of fallen seeds and other debris. Dung samples were individually dissected and broken apart, placed on a fine-mesh sand sieve (0.085 mm) and carefully strained to wash off dirt, to visibility see and collect the seeds. We then harvested and identified the seeds of alien invasive *Lantana camara*, *Solanum mauritianum*, *Melia azedarach* and *Opuntia monacantha*, and properly stored the seeds in labelled glass vials.

3.3.5 Data analyses

We analysed the data from the dung deposition survey using a Pearson Chi-square to compare frequencies of dung samples deposited across the different microhabitats among the ungulate species. We used General Linear Model Analysis of Variance (ANOVA) to test for differences in seed composition in dung piles between (1) ungulate species, (2) microhabitats, (3) alien invasive plants, and (4) sites. Data were not normally distributed, therefore \log_{10} transformed before ANOVA analyses. Post-hoc tests performed to investigate for further significant differences between variables. We could not correctly give a complete account of temporal variations in seed deposition because of the nature of our data collection; however, we have graphically represented variations in seed deposition for the months in which our data were collected (Supplementary information Figure S3.1). We conducted all statistical analyses using IBM SPSS Statistics (SPSS Inc, version 27, USA).

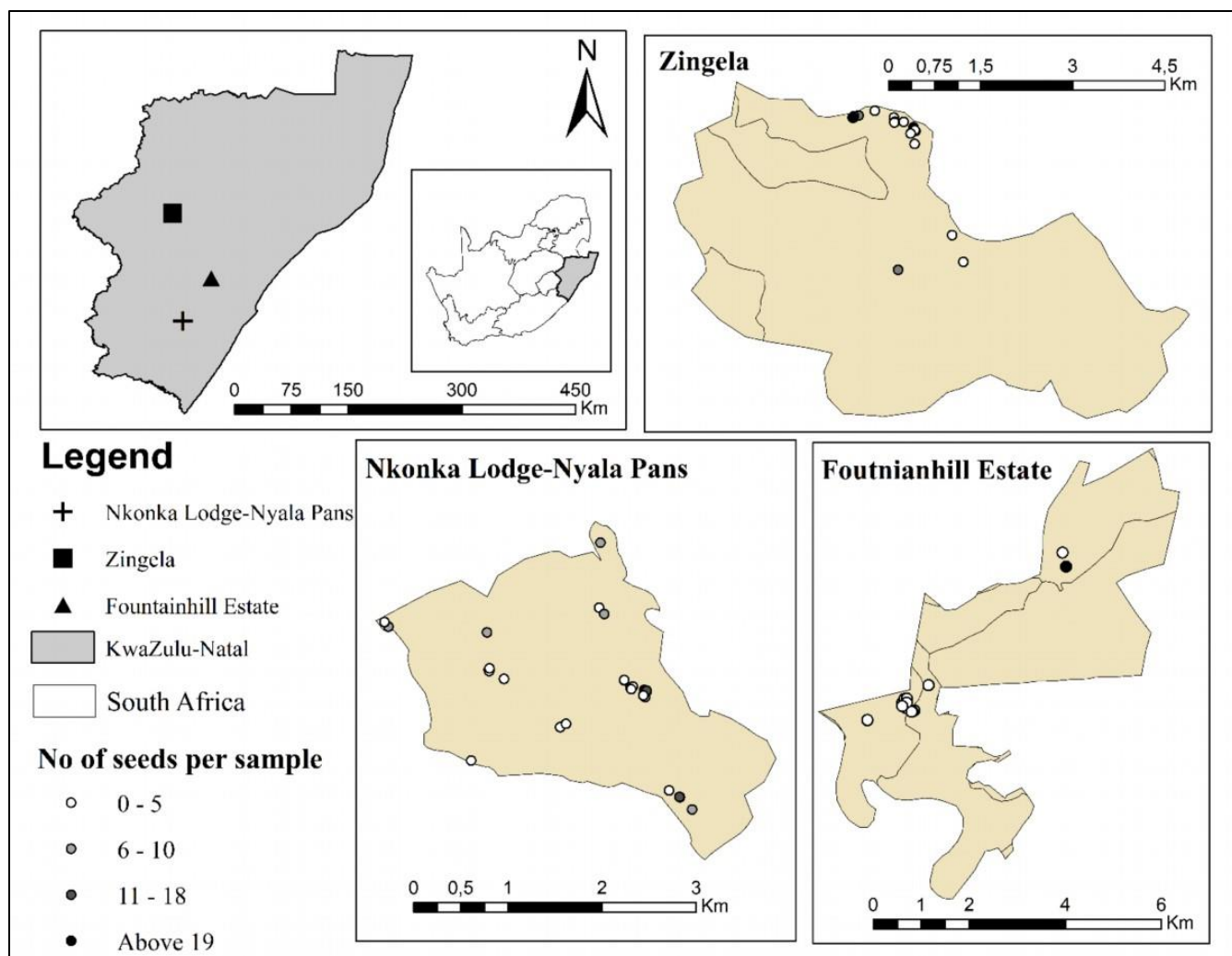


Fig. 3.1. Study sites and spatial representation of seeds of the fleshy-fruited alien invasive plants per dung pile for the present study, in KwaZulu-Natal, South Africa.

3.4 Results

During the dung depository survey, we recorded and identified a total of 2726 dung piles from nine different ungulate species (Table 3.1). The Pearson Chi-square analyses showed significant differences ($p < 0.001$) in dung deposition frequency between different ungulate species (Table 3.1; bushbuck *Tragelaphus sylvaticus*: $\chi^2 = 58.46$, $df = 4$; impala *Aepyceros melampus*: $\chi^2 = 204.58$, $df = 4$; greater kudu *Tragelaphus strepsiceros*: $\chi^2 = 162.23$, $df = 4$; nyala *Tragelaphus*

angasii: $\chi^2 = 175.27$, $df = 4$; common warthog *Phacochoerus africanus*: $\chi^2 = 65.44$, $df = 4$; giraffe *Giraffa camelopardalis*: $\chi^2 = 246.16$, $df = 4$; common duiker *Sylvicapra grimmia*: $\chi^2 = 33.16$, $df = 4$; blue wildebeest *Connochaetes taurinus*: $\chi^2 = 151.80$, $df = 3$; zebra *Equus quagga*: $\chi^2 = 17.78$, $df = 2$). Impala ($n = 941$) and bushbuck ($n = 333$) dung piles were the most common, and common duiker ($n = 62$) and zebra ($n = 71$) dung piles were the least common. Similarly, the Pearson Chi-square analyses showed significant differences ($p < 0.001$) in overall dung deposition frequency across microhabitats (Table 3.2; savannah: $\chi^2 = 400.464$, $df = 8$; grassland: $\chi^2 = 661.416$, $df = 8$; thicket: $\chi^2 = 112.197$, $df = 7$; woodland: $\chi^2 = 812.856$, $df = 6$; degraded woodland: $\chi^2 = 236.372$, $df = 7$). In all the habitats, impala dung piles were the highest, except for the thicket microhabitat where nyala deposited the most dung piles. The results showed that the savannah ($n = 1008$; 37%) and grassland ($n = 616$; 22.6%) received the highest deposition of dung piles, and degraded woodland ($n = 223$; 8.2%) the lowest deposition of dung piles (Fig. 3.2).

We collected a total of 271 fresh dung piles (Zingela: $n = 52$; FHE: 105; NLNP: 114), summing to 54.61 kg (wet faecal mass). The number of seeds per dung piles varied significantly among ungulate species (ANOVA: $F = 2.756$; $df = 7$; $p = 0.012$). Data showed that bushbuck ($n = 144$), greater kudu ($n = 113$) and nyala ($n = 66$) contained the highest number of seeds of alien invasive plants per dung pile. We found the lowest number of seeds per dung pile for common warthog ($n = 2$) and common duiker (8). We found no seeds of fleshy-fruited alien invasive plants in the dung of zebra (Fig. 3.3a). The number of seeds per dung pile deposited between microhabitats significantly varied (ANOVA: $F = 2.560$; $df = 4$; $p = 0.04$). There was higher seed deposition in the savannah ($n = 273$) and thicket ($n = 111$) microhabitats. Degraded woodland ($n = 14$) and woodland ($n = 22$) microhabitats received the lowest number of seeds (Fig. 3.3b). The number of fleshy-fruited alien invasive plant seeds varied per dung pile (ANOVA: $F = 14.191$; df

= 2; $p = 0.001$), with *S. mauritanum* ($n = 205$) being the most abundant than *L. camara* ($n = 138$) and *O. monacantha* ($n = 108$). Seeds of *M. azedarach* were not found in any of the dung piles collected (Fig. 3.3c). The number of seeds per dung pile varied between the sites (ANOVA: $F = 5.249$; $df = 2$; $p = 0.007$), with higher numbers in NLNP ($n = 255$) and Zingela ($n = 149$) then FHE ($n = 47$) (Fig. 3.3d). Temporal variations in seeds deposited varied between the months when our data were collected (Supplementary information Figure S3.1), with July ($n = 255$; $\bar{x} = 5.80$) and June ($n = 111$; $\bar{x} = 3.83$) receiving the highest seed deposition, and August ($n = 6$; $\bar{x} = 2$) the lowest seed deposition (Supplementary information Figure S3.1).

Table 3.1. Pearson Chi-square (χ^2) of dung deposition by ungulate species for the present study in KwaZulu-Natal, South Africa.

Chi-square	Ungulate species								
	Bushbuck	Impala	Greater kudu	Nyala	Common warthog	Giraffe	Common duiker	Blue wildebeest	Zebra
χ^2	58.46	204.58	162.23	175.27	65.44	246.16	33.16	151.80	17.78
df	4	4	4	4	4	4	4	3	2
p-value	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001

Table 3.2. Pearson Chi-square (χ^2) of dung deposition in the different microhabitats in the present study.

Chi-square	Microhabitats				
	Savannah	Grassland	Thicket	Woodland	Degraded woodland
χ^2	404.464	661.416	164.682	812.856	236.372
p-value	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
df	8	8	8	6	7

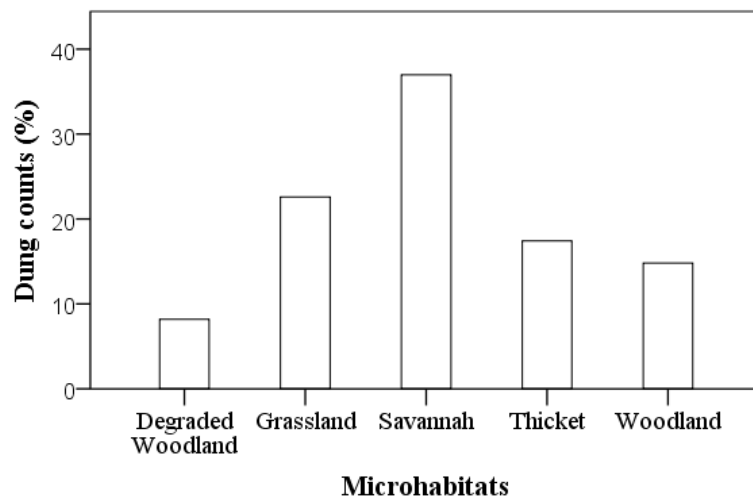
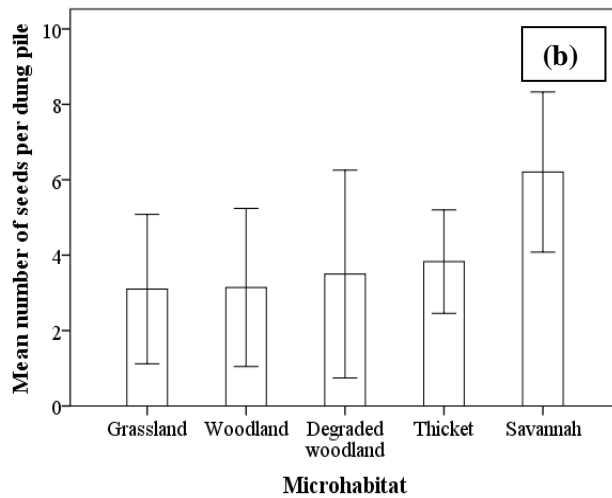
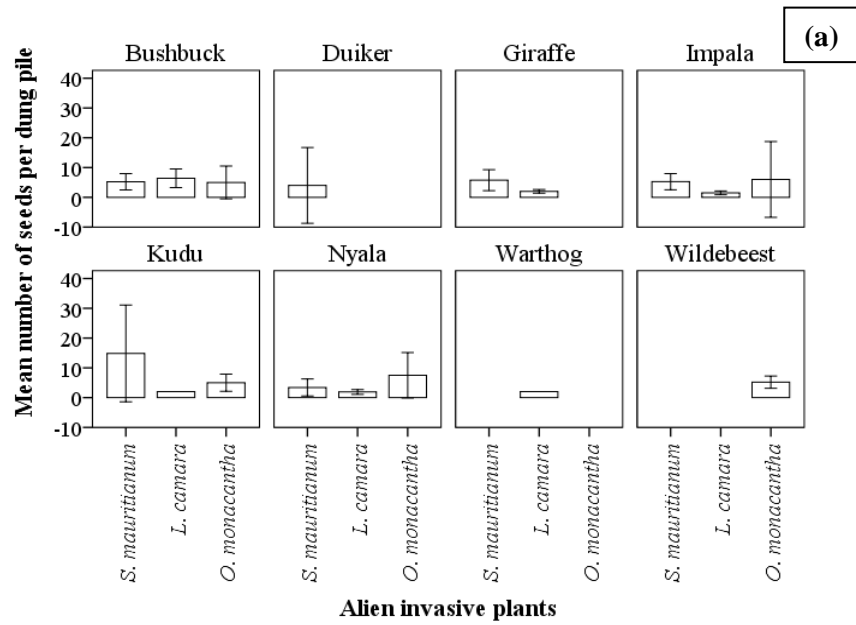


Fig. 3.2. Overall dung count (%) in the different microhabitats in the present study, in KwaZulu-Natal, South Africa.



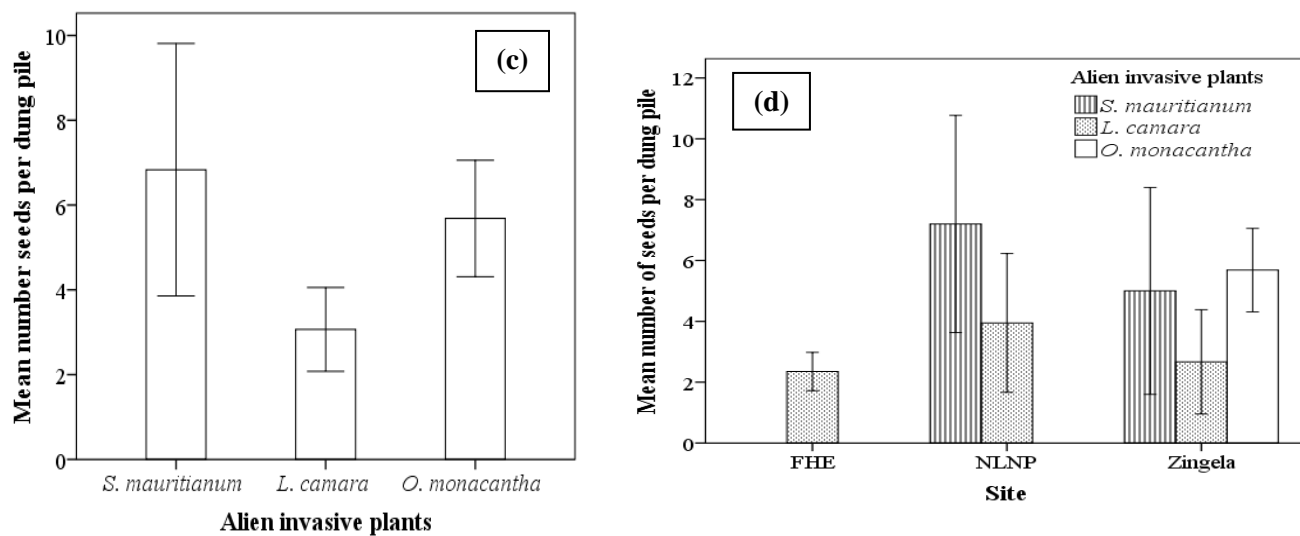


Fig. 3.3. Seed content in per dung pile, and their variations between (a) ungulate species, (b) habitats, (c) alien invasive plant species, and (d) sites in the present study. The error bars (mean \pm SD) were set at a 95% confidence interval.

Table 3.3. Summary of fleshy-fruited alien invasive seeds (lantana, *L. camara*; bugweed, *S. mauritianum*; syringa, *M. azedarach*; prickly-pear, *O. monacantha*) found in fresh dung pile samples of wild southern African ungulates in the present study, KwaZulu-Nata, South Africa.

	Collected faecal samples (samples with seeds) (n)	Total faecal wet mass (kg)	Seed composition per dung pile				
			Lantana	Bugweed	Syringa	Prickly-pear	Mean \pm SD per dung pile sample
Bushbuck	40 (18)	4.11	77	47	0	20	5.76 \pm 4.156
Common duiker	9 (2)	0.29	0	8	0	0	4 \pm 1.414
Giraffe	26 (9)	6.99	24	23	0	0	2.94 \pm 2.112
Impala	28 (16)	1.97	12	21	0	12	3.21 \pm 2.326
Greater kudu	25 (8)	4.84	4	89	0	20	9.42 \pm 11.958
Nyala	20 (13)	1.78	19	17	0	30	3.47 \pm 3.255
Common warthog	43 (1)	6.74	2	0	0	0	2 \pm 0
Blue wildebeest	57 (5)	14.48	0	0	0	26	5.20 \pm 1.643
Zebra	23 (0)	13.41	0	0	0	0	-

3.5 Discussion

Large herbivorous mammals are among frugivorous species responsible for transporting seeds across various habitats, facilitating the colonisation of vacant niches (Baltzinger et al., 2019). We conducted a dung depository survey to potentially predict microhabitats vulnerable to alien plant invasion, based on dung deposition counts in each microhabitat. The results showed dung deposition counts varied among ungulate species. A study by Malo et al. (2000) showed that ungulate dung deposition also varied among ungulates, with large-bodied ungulates (i.e. cattle, *Bos taurus*) contributing the largest percentage in the deposition of dung and seeds. In the present study, impala and bushbuck dung piles were the most common, and common duiker dung piles were the least common. This may be a consequence of high species abundance and low species abundance, respectively. Although bushbuck, nyala, common duiker and greater kudu are highly elusive species (Downs et al., 2016; Ehlers Smith et al., 2017; Zungu et al., 2020.), using a non-invasive sampling technique such as dung counts enabled us to indirectly detect these elusive species as they are physically difficult to observe (Smith, 2016).

Dung deposition counts also varied across the different microhabitats. In all the microhabitats sampled for the purpose of this study, impala dung counts contributed the highest number, except for the thicket microhabitat where nyala deposited the most dung samples. The savannah microhabitat showed the highest dung deposition percentage between all the sites. Similarly, Malo et al. (2000) reported high dung deposition in open habitat. Therefore, this suggests that open habitats such as the savannah microhabitats may be prone to plant alien invasion. Moreover, Bitani et al. (2020) predicted that fleshy-fruited alien invasive plants of open

habitats such as *S. mauritianum* and *L. camara* are potentially effectively dispersed. High dung deposition in the savannah and grassland microhabitats may also be influenced by habitat occupancy and resource availability (Malo and Suárez, 1995a, 1995b; Malo et al., 2000; Ofstad et al., 2016). Ungulate species select habitats to occupy based on habitats that offer food resources to meet their metabolic requirements (Jarmen, 1974; Demment and van Soest, 1985). Moreover, when conducting a dung depository survey, dung decay must be considered (Jenkins and Manly, 2008; Hibert et al., 2008; Smith, 2016). Therefore, ungulate species recorded were those with dung defecation that was identifiable during the survey. Dung pile samples that could not be identified were not considered in the survey, to minimise dung misidentifications. However, this might have eliminated the inclusion of other ungulate species and limited dung count sample size.

The number of seeds found per dung pile varied significantly among ungulate species, with dung pile samples of greater kudu, bushbuck and nyala containing the greatest number of alien invasive seeds. Greater kudu and bushbuck are browsers and selective feeders (Estes, 1991), and therefore, they may potentially select fruits when browsing foliage is low in quality. There were fewer seeds per dung pile of common warthog and common duiker. No fleshy-fruited alien invasive plant seeds were found in dung piles of zebra. The lower number of seeds in dung piles of common duiker may be because of a smaller sample size of dung piles. Common warthog and zebra are roughage grazers (Estes, 1991), with a diet highly based on grass species to meet metabolic requirements (Clauss et al., 2013), therefore potentially rarely ingest fruits or completely digesting seeds in the case of fruits ingestion. The number of seeds per dung pile deposited between microhabitats varied significantly, with significances greater between grassland-savannah and

savannah-thicket microhabitats. There was higher seed deposition in the savannah and thicket microhabitats, respectively. Degraded woodland and the woodland microhabitats received the lowest number of seeds per dung pile. The degraded woodland microhabitat was only identified in one of the study sites (Zingela). Therefore, if data for woodland and degraded woodland were combined to form woodland microhabitats, the grassland microhabitats received the lowest amount of seed deposition per dung pile. A large proportion of viable seeds are defecated in habitats predominately occupied by frugivores (Wenny, 2001; D'hondt et al., 2012). Potentially, habitats occupied by frugivores that ingest and disperse invasive alien plants become vulnerable to alien plant invasion (Cosyns et al., 2005).

The number of seeds per dung pile varied among the fleshy-fruited alien invasive plants, and significant differences were observed for all plant species except between *L. camara* and *O. monacantha*. More seeds of *S. mauritianum* were found in dung piles than *L. camara* and *O. monacantha*. No seeds of *M. azedarach* were found in any of the dung pile samples. Small seeds produced in copious numbers (e.g. *S. mauritianum*) in fruits pass through the gut of ungulates frequently (Mouissie et al. 2005), compared with relatively larger seeds in single-fruits (e.g. *L. camara* and *O. monacantha*) that are subjected to repeated mastication and retained longer in the gut passage (Prasad et al. 2006). Therefore, larger seeds are potentially destroyed more than smaller seeds. This was also evident in by-catch of various larger seeds of acacia *Vachellia* species found in the faecal droppings (Miller, 1994, 1996). The number of seeds per dung pile varied between the sites, with significant differences for all sites except between Zingela and NLNP. Because *O. monacantha* was only found in Zingela, it added an invasive plant species that was not

present in other sites; therefore, increasing the number of seeds per dung pile. Essentially, when we excluded *O. monacantha* from the analyses and only compared the seed composition of *L. camara* and *S. mauritianum*, the NLNP site reported a higher seed deposition than any of the sites. In the Mediterranean Dehesa, a mixture of livestock and wild ungulate farming showed that dung piles of cattle *Bos taurus* contained the highest number of seeds and species richness (Malo and Suarez, 1995a). In the NLNP, a mixture of livestock and wild ungulates farming is also practised, and it was the site with the highest seed deposition of *L. camara* and *S. mauritianum*. For this, we recommend a comparative analysis between domestic and wild ungulates on the dispersal of fleshy-fruited alien invasive plants. Therefore, farmers need to be aware of the possible accelerated rate of plant invasion in farms with a combination of domestic and game ungulates.

Our main aim of the present study was to predict microhabitats vulnerable to alien plant invasion by conducting a dung depository survey of ungulate species and give an account of seed composition of fleshy-fruited alien invasive *L. camara*, *S. mauritianum*, *M. azedarach* and *O. monacantha* through faecal content analyses. Our results showed that ungulate defecation counts varied among ungulates and among microhabitats. Both the high dung deposition and high seed deposition suggested the savannah habitat as the most vulnerable to alien plant invasion. The dung deposition survey showed that woodland is the second most vulnerable, but the seed deposition showed that degraded woodland is the second most vulnerable. Essentially, both these habitats are similar, they were only separated for the purpose of this study. Simultaneously the study may have suggested that savannah and woodland microhabitats may be potentially vulnerable to plant invasions. We recommend a seed deposition survey over consecutive sampling periods to

determine temporal and spatial variations in seed deposition of alien invasive plants. Advantageously, the dissection of dung pile samples reveals viable (intact seeds) and non-viable (destroyed through crushing), beneficial when conducting germination trials (Malo et al., 2000). Dissecting large amounts of dung pile samples, as we have done for the present study, limited the quality of the dung samples for a germination trial because of the time invested in processing the dung pile samples for extraction of seeds. Dung pile samples were stored in the freezer for longer periods until processed. By-catch data in dung pile samples predominately comprised of seeds of various acacia *Vachellia* species. Generally, seeds from fleshy-fruits display a greater seed germination enhancement post-gastric than seeds from dry-podded fruits (Traveset and Verdú, 2002). However, we recommend further research that would compare if ungulates are effective dispersers of fleshy-fruited or dry-podded seeds of alien invasive plant species. Given the accelerated rate of biodiversity loss because of plant invasions, the prediction of habitats vulnerable by increased plant invasions can be useful for ecosystem management.

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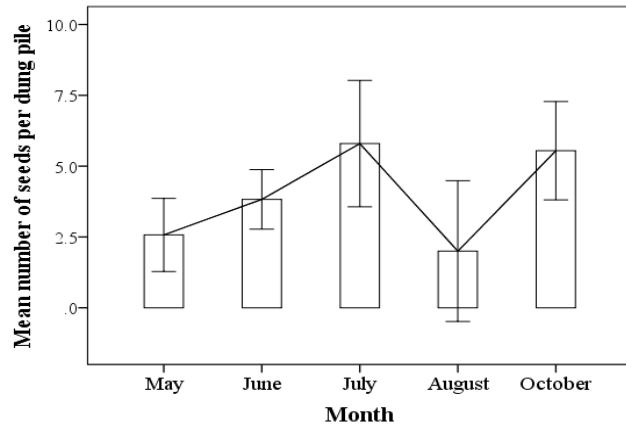
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3.8 Supplementary information



Supplementary information Figure S3.1. Temporal variation of seeds of fleshy-fruited invasive plants per dung pile of wild southern African ungulate species, in the present study in KwaZulu-Natal, South Africa. The error bars (mean \pm SD) were set at 95% confident interval.

Supplementary information Table S3.1. Description of microhabitat type based of vegetative composition and structure, for the present study. Microhabitat were classified according to Kleynhans et al. (2011) and Mucina and Rutherford (2011).

Microhabitat type	Characteristic
Grassland	Dominated by grasses (Poaceae) and <25% encroached by woody plant species. In the study sites, plain grass zone patches on the periphery of savannah and thicket microhabitats were considered as grassland, irrespective of their size.
Savannah	Predominantly a bushveld representative rather than a distinctive tree-grass layer. Dominated by irregular distribution of small trees and tall shrubs, often low-lying open canopies. Specifically in the study sites, this microhabitat was also characterised not only with grass layer as ground cover, but also with ground creeping plant species and often bare ground because of erosion.
Thicket	Woody vegetation of >75% shrubs and trees that form dense and impenetrable stands. In the study sites, thicket microhabitat was predominately dense stands of <i>L. camara</i> mixed with other shrub species.
Woodland	Sparsely distributed mature trees with non-overlapping open canopies. In the study sites, the microhabitat was also characterized by a grass-layer or small shrub-layer below mature trees.
Degraded woodland	In the study sites, the degraded woodland microhabitat were the same vegetative characteristics as woodland, but highly eroded and invaded with <i>O. monacantha</i> , therefore separately classified.

CHAPTER 4

Potential mean retention time and seed dispersal distance of wild southern African ungulates in KwaZulu-Natal, South Africa

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Running header: Potential retention times and dispersal distances by ungulates

4.1 Abstract

The distance to which seeds may be dispersed and the extent to which seeds are retained in the gut passage of large mammalian species is variable, depending on numerous intrinsic and extrinsic factors. Therefore, proxies have been established to estimate dispersal distances and mean retention times of large mammals using allometric scaling derivations. We investigated the role of wild southern African ungulates on seed dispersal by estimating potential mean retention time (h) and dispersal distance (km) of fleshy-fruited alien invasive *Lantana camara*, *Solanum mauritianum* and *Opuntia monacantha*. To quantify this seed dispersal relationship, various ungulate characteristics, such as body mass (BM, kg), home range (HR, km²), and daily movement distance (DMD, km) were used to estimate potential mean retention time (MRT, h) and seed dispersal distances (km). Data for ungulate BM (kg) were sourced from published literature, and data on MRT (h), HR (km²), DMD (km) and dispersal distances (km) were obtained using allometric scaling equations. MRT (h) varied among ungulates, influenced first by gut physiology and then BM (kg). For this reason, hind-gut fermenters had the shortest retention time than ruminants, and within each digestive physiology group, MRT (h) was then influenced by BM (kg). Potential dispersal distances were estimated using HR (km²) and DMD (km) as distance variables. Potential dispersal distance using HR (km²) as a distance factor generated a dispersal distance range of 37.45 – 557.22 km, and 45.52 – 248.98 km when using DMD (km). Ungulate species with relatively smaller BM (kg) were observed to have shorter dispersal distances, and the opposite was found for ungulates with relatively larger BM (kg). We recommend further research on the derivation of allometric equations for modelling dispersal distance of ungulate species to include the aspect of MRT (h) as a function of gut physiology, as the parameter proves to be significant for predicting dispersal distances. Ultimately, estimating retention times and dispersal distances of

ungulate species is essential for conservation purposes, and may be potentially used for effective management of alien invasive plants.

Keywords: Ungulate-mediated dispersal, dispersal distances, mean retention time, allometric scaling, body mass, home range

4.2 Introduction

The functioning of terrestrial ecosystems is dependent on herbivorous mammalian species (Georgiadis & McNaughton, 1990; Malo & Suárez, 1995; Pellerin et al., 2016), performing as ecosystem drivers of plant communities (Malo et al., 2000; Albert et al., 2015). The role of herbivorous mammals pertains to seed dispersal (Janzen, 1984), a critical process that influences plant populations' dynamics and species composition (Pellerin et al., 2016). Fundamentally, seeds ingested by frugivores pass through the gut (endozoochory) to promote seedling establishment away from the parent plant, facilitating the ability of seeds to colonise vacant niches (Janzen, 1984; Schupp et al., 2010). However, among other factors, seed retention time within the gut of seed vectors (Mouissie et al., 2005; Picard et al., 2015), spatial movement, and distances travelled by seed vectors (Sutherland et al., 2000; Nathan et al., 2008; Will & Tukernberg, 2008; Côrtes & Uriarte, 2013; Rehm et al., 2019) collaboratively influence the distance to which seeds may be dispersed. Moreover, differences in dispersal distances among large herbivorous species may be influenced by the ecological traits exhibited both by seed vectors and plant species (Côrtes & Uriarte, 2013).

Seed survival in the gut passage of large herbivorous ungulates is influenced by seed retention time, the time taken by seeds to pass through the gut (Pellerin et al., 2016); therefore,

affecting dispersal distances of plant species (Picard et al., 2015). Consequently, seed retention time is a facilitation factor for seed dispersal (Janzen, 1984), and in the case of ungulates, dependent on gut physiology (Steuer et al., 2011; Picard et al., 2016) and body mass (Demment, 1983; Demment & van Soest, 1983; Illius & Gordon, 1992). Essentially, ruminants display longer retention times than hindgut fermenters (Bell, 1971; Owen-Smith, 1988; Kleynhans et al., 2011; Steuer et al., 2011). Moreover, among ruminants, browsers display shorter retention times than grazers of similar body size (Hofmann, 1989; Clauss et al., 2005). Allometric scaling relationship between body mass and retention time implies that larger herbivores retain seeds in their gut for longer periods (Demment & van Soest, 1985; Illius & Gordon, 1992; Müller et al., 2013). Moreover, the linearity relationship of body mass and dispersal distances has shown that the body mass of seed vectors affects their potential dispersal distances (Bowman et al., 2002; Sutherland et al., 2000; Santini et al., 2013). Additionally, seed traits are potentially responsible for some of the variation in seed retention times (Traveset, 1998; Donatti et al., 2007; D'hondt & Hoffmann, 2010), as a result of seed survival in the gut passage being highly affected by seed traits (Clauss et al., 2004; Bruun & Poschlod, 2006; Kleyheeg et al., 2018). Ideally, small seed size, hard seed coat, low seed mass and round seed shape experience shorter seed retention time within the gut passage (Bruun & Poschlod, 2006; Picard et al., 2015); subsequently, larger seeds experience longer seed retention time (Clauss et al., 2005; Picard et al., 2016). However, the empirical evidence of seed retention time for dispersal purposes by ungulate species is limited in literature, except for relatively few studies (Cosyns et al., 2005; Mouissie et al., 2005; Seefeldt et al., 2010; Picard et al., 2015). The paucity is primarily because of extreme logistic efforts pertaining to the experimental aspects of obtaining seed retention time data of ungulate species. Therefore, the

derivation of allometric scaling equations have been used instead to potential estimate mean retention times.

Dispersal distances are highly variable between species and even within populations of the same species (Santini et al., 2013). The majority of the time, individuals facilitate frequent short dispersal distances and occasionally contribute to long seed dispersal distances (Howe & Smallwood, 1982; Nathan et al., 2003; Nathan et al., 2008). Although short dispersal distances emphasise localized ecosystem functioning, long dispersal distances influence the plant community's temporal and spatial metapopulation dynamics (Nathan et al., 2003; Santini et al., 2013; Pellerin et al., 2016). Because large herbivores, such as ungulates, have larger home ranges (Bowman et al., 2002), they are reported to disperse seeds long distances (Vellend et al., 2003; Myers et al., 2004; Sridhara et al., 2016). In the case of seed dispersal, seeds can be dispersed over longer distances (Nathan et al., 2008; Bullock et al., 2011). Therefore, the travelling of long distances promotes gene flow between distant habitats and, consequently, seed dispersal (Cain et al., 2000; Pellerin et al., 2016), especially in fragmented landscapes (Picard et al., 2016). Consequently, the dispersal of seeds over long distances is advantageous for plant species' long-term persistence (Cain et al., 2000; Nathan et al., 2008; Pellerin et al., 2016). Non-volant terrestrial species are believed to disperse seeds over greater distances than arboreal species because of tree canopy discontinuity (Santini et al., 2013). However, the dispersal distances by terrestrial species may vary and be limited by constraining factors, such as boundary enclosures (Slater & du Toit, 2002). A combined effort of representing animal movements and gut passage rate determines the seed shadow (how far a seed can potentially be dispersed) (Brodie et al., 2009a, 2009b; Sridhara et al., 2016), fundamental for seed dispersal distance estimations (Westcott & Graham 2000; Westcott et al., 2005; Pellerin et al., 2016).

Importantly, dispersal distance by frugivorous species that disperse alien plants potentially influences the rate of alien plant invasion (Corlett, 2009). Therefore, as ungulates are potential contributors to plant invasions, information on ungulate-mediated seed dispersal distances is mandatory for predictive measures of future plant distributions (Nathan et al., 2008). Thus, a collective comprehensive understanding of daily movement distances, home ranges, and mean retention times of ungulates are important when predicting future distribution and dispersal patterns of invasive alien plant species. Our present study aimed to estimate potential mean retention time (h) and seed dispersal distances of wild southern African ungulate species that potentially disperse fleshy-fruited alien invasive plants. Estimations were based on ungulate body mass (BM in kg), home range (HR in km²) and daily movement distance (DMD in km), as variables manipulated in allometric scaling equations. Our objectives of this study were to (1) estimate the mean retention time (h) of ungulate species and (2) to estimate potential dispersal by the ungulates based on allometric scaling. We predicted that large-bodied ungulate species would disperse seeds further and retain seeds longer in their gut passage.

4.3 Methods

4.3.1 Parameters used for estimating potential mean retention time (h) and potential dispersal distances (km)

We estimated potential dispersal distances (km) and potential mean retention time (h) of ungulate species observed consuming alien invasive plants (as per Chapter 2) and of ungulate species where dung piles contained seeds of *Lantana camara*, *Solanum mauritianum* and *Opuntia monacantha* (as per Chapter 3). Body mass (BM) of ungulates were impractical to be measured for this study; therefore, they were sourced from Kingdon and Hoffmann (2013) and Skinner and Chimimba

(2005) as both sources represented the most comprehensive summaries of BMs of southern African mammals. However, in cases where BM (kg) of a particular ungulate species was not clearly stated in these (Kingdon & Hoffmann, 2013; Skinner & Chimimba 2005), additional literature was considered (Supplementary information Table S4.1). Additionally, to increase BM (kg) sample size, additional BM (kg) data were sourced post the publications of Kingdon and Hoffmann (2013), and Skinner and Chimimba (2005), generating average BM (kg) for each ungulate species (Supplementary information Table S4.1). For each ungulate species, the BMs (kg) of males and females were averaged to obtain an overall BM (kg). According to the Jarmen-Bell Principle, BM (kg) allometry in dimorphic ungulates slightly affects retention time; however, the differences are insignificant (Pérez-Barbería et al., 2008; Clauss et al., 2008). Moreover, the dimorphic factor of certain mammal species has an insignificant difference when modelling dispersal distances (Santini et al., 2013).

Home range (HR, in km²) of some ungulates (i.e. zebra: *Equus quagga*, impala: *Aepyceros melampus*, greater kudu: *Tragelaphus strepsiceros*, giraffe: *Giraffa camelopardalis* and blue wildebeest: *Connochaetes taurinus*) were obtained from published literature (Smuts, 1975; Murry, 1982; du Toit, 1990; Fennessy 2009; Bartlam-Brooks et al., 2013; Deacon 2015; Kingdon 2015; McQualter et al. 2015; Deacon & Smith 2017; Selebatso et al. 2017; Supplementary information Table S4.1), where HR (km²) was empirically obtained using device method of global positioning system (GPS) tagging. Consideration was given to literature where HRs (km²) were estimated using a 95% or 100% minimum convex polygon (MCP), as other home range estimation methods were limited in literature, particularly for ungulate species in this study. Since substantial evidence of HR (km²) was limited for the rest of the ungulate species, their HR (km²) were estimated using appropriate equations scaling to BM (kg). HR (km²) equation was derived from du Toit (1990):

$$[A_{hr} = 0.024 (BM)^{1.38}] \quad [1]$$

where A_{hr} is home range area (km^2), BM is body mass (kg), 0.024 and 0.18 are allometric constants. We found the HR (km^2) equation by du Toit (1990) [equation 1] suitable for the purpose of this study, as it was empirically derived from ungulate species in South Africa, including giraffe, greater kudu, and impala. Therefore, on that reasoning, the du Toit (1990) HR (km^2) equation was preferable for this study.

Substantial evidence of DMD (km) by GPS tagging was limited for the study ungulate species; therefore, DMD (km) were estimated using appropriate equations scaling to BM (kg). DMD equation was derived from Carbone et al. (2005):

$$[DMD = (BM)^{0.34}] \quad [2]$$

where DMD is daily movement distance (km), BM is body mass (kg), 0.024 and 0.18 are allometric constants. DMD (km) by ungulate species is highly variable, depending on seasonality (McQualter et al., 2015), age and sexual dimorphism (Sutherland et al., 2000; Saïd et al., 2005), body mass (Garland, 1983), dietary type and herd size (Carbone et al., 2005), and survival resource availability, such as food and water, within the occupied habitat type (Smuts, 1975; Cumming & Cumming 2003). Therefore, DMD (km) equation by Carbone et al. (2005) [equation 2] was preferable for this study as body mass, dietary type, and herd size were inclusive factors in the derivation of the equation.

4.3.2 Estimating potential dispersal distances

To estimate potential dispersal distances, ungulate characteristics, such as body mass (BM in kg), home range (HR in km^2) and daily movement distance (DMD in km), were used as proxies. Potential dispersal distances were estimated using two approaches: HR (km^2) and DMD (km) as

the main variables of manipulating distance. Using an allometric equation from Santini et al. (2013), dispersal distance was first estimated by means of HR (km²), as follows:

$$[MDD_{HR} = 13.11(BM^{0.34}) (HR^{0.27})] \quad [3]$$

where MDD is the maximum dispersal distance (km), BM is body mass (kg), HR is home range (km²), 0.34 and 0.27 are allometric constants. We further manipulated the equation [equation 3] and substituted home range with daily movement distance to estimate dispersal distance by means of DMD (km), as follows:

$$[MDD_{DMD} = 13.11(BM^{0.34}) (DMD^{0.27})] \quad [4]$$

where MDD is the maximum dispersal distance (km), BM is body mass (kg), DMD is daily movement distance (km), 0.34 and 0.27 are allometric constants. Of the 16 ungulate mammals used in Santini et al. (2013) to derive the equation, six ungulates were of African descent. In consideration of diverse factors affecting dispersal distance, we found the equation by Santini et al. (2013) the most suitable as variables such as body mass, home range, locomotion type (movement speed and energy cost), diet type, habitat breadth, territorial and social behaviour were included in the derivation of the dispersal distance equation. Considering that these determinants of seed dispersal may reduce or expand the actual dispersal distance, results of potential dispersal distances were therefore presented as an estimation dispersal distance for each ungulate species.

4.3.3 Estimating potential mean retention times

Experimental assessments of mean retention time (MRT, h) of wild ungulates are rare in the literature, as they are difficult to obtain, except for wild captive ungulates (Mouissie et al., 2005; Seefeldt et al., 2010; Picard et al., 2015); therefore MRT (h) could not be empirically obtained for

this study. To estimate mean retention time (MRT in h), ungulate body masses (BM in kg) were used in allometric scaling equation from Steuer et al. (2011) as follows:

$$[\text{MRT} = 29.1(\text{BM})^{0.12}] \text{ for ruminants} \quad [5]$$

where MRT is the mean retention time (h), BM is body mass (kg), 29.1 and 0.12 are allometric constants, and

$$[\text{MRT} = 31.0(\text{BM})^{0.01}] \text{ for hindgut fermenters (non-ruminants)} \quad [6]$$

where MRT is the mean retention time (h), BM is body mass (kg), 31.0 and 0.01 are allometric constants. Gut physiology significantly influences MRT (h) (Demment & van Soest 1983; Illius & Gordon 1992); therefore, the equations were distinctively used to accommodate the differences in gut physiology of ungulates. In the study by Steuer et al. (2011), equations were derived based on gut physiology of ungulate species by considering a total of eight ruminants and six hindgut fermenters, which a total of 110 ungulate species are of African descent. We acknowledge that significant allometric scaling equations have been formulated (Demment, 1983; Demment & van Soest, 1985; Illius & Gordon, 1992; Clauss et al., 2007); however, equations by Steuer et al. (2011) are relatively recently formulated using empirical data, and not based on theoretical calculations. Furthermore, we acknowledge that obtaining MRT (h) using allometric scaling equations does not consider important determinants, such as individual behaviour, age, and ingested seed morphology. Considering that these determinants may reduce or expand the actual MRT (h), results were therefore potentially presented as an estimation.

4.3.3 Statistical analyses

We used MRT (h) data to determine variations in retention time between ungulate species. According to du Toit (1990), a linear relationship exists between BM (kg) and HR (km²) for wild

southern African ungulates. Similarly, a linearity relationship was performed between BM (kg) and HR (km²), and additionally between BM (kg) and DMD (km) to determine their relationship with BM (kg) for estimating potential dispersal distances. Due to the lack of normality of the data, BM (kg), HR (km²) and DMD (km) were log₁₀ transformed, and a linear regression test was performed. All statistical analyses were conducted using IBM SPSS Statistics (SPSS Inc, version 27, USA).

4.4 Results

There was a substantial variation in MRT (h) between ungulates. Results of MRT (h) of ungulates suggested that it was influenced by digestive physiology more than by BM (kg). Therefore, showing that hind-gut fermenters, common warthog *Phacochoerus africanus* and zebra, had the shortest MRT (h) of 32.33 h and 32.89 h, respectively. Among ruminants, common duiker *Sylvicapra grimmia* and bushbuck *Tragelaphus sylvaticus* showed the shortest MRT (h) of 41.14 h and 45.86 h, respectively; and blue wildebeest and giraffe showed the longest MRT (h) of 55.38 h and 65.94 h, respectively (Fig. 4.1). The linear regression showed that there is a strong relationship between BM (kg) and DMD (km) (Figure 4.2a; $R^2 = 0.999$; $F = 10372.58$; $p < 0.001$; $df = 1$), and between BM (kg) and HR (km²) of ungulate species (Figure 4.2b; $R^2 = 0.967$; $F = 202.202$; $p < 0.001$; $df = 1$). The linear relationship showed ungulate species with a small BM (kg) travel the shortest daily distances. They have the smallest home range (e.g. common duiker), compared with ungulates with a larger BM (kg) that travel the longest daily distances and occupy larger home ranges (e.g. giraffe). Based on the linearity relationships, the estimated dispersal distances followed the same trend (Figure 4.2; Figure 4.3). Potential dispersal distance using HR (km²) generated a dispersal distance range of 37.45 – 557.22 km and 45.52 – 248.98 km when

using DMD (km). When evaluating the two distance variables (HR, in km² and DMD, in km) used to estimate dispersal distance, there was no considerable variation in potential dispersal distance for ungulate species with relatively smaller BM (kg). These species are common duiker, bushbuck, impala, common warthog and nyala. However, potential dispersal distance may vary as BM (kg) increases, particularly observed for greater kudu, blue wildebeest, zebra and giraffe, respectively.

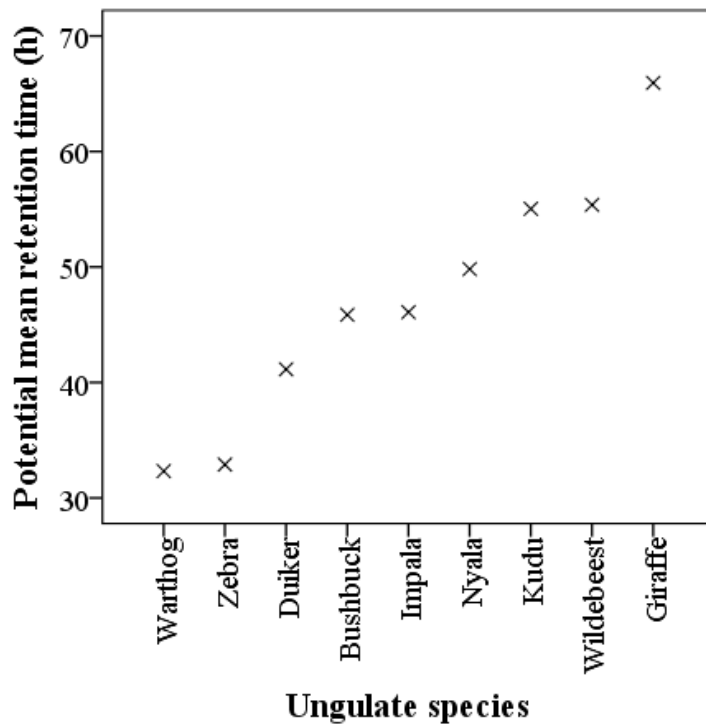


Figure 4.1. Estimated mean retention time (h) of wild southern African ungulate species in the present study in KwaZulu-Natal, South Africa.

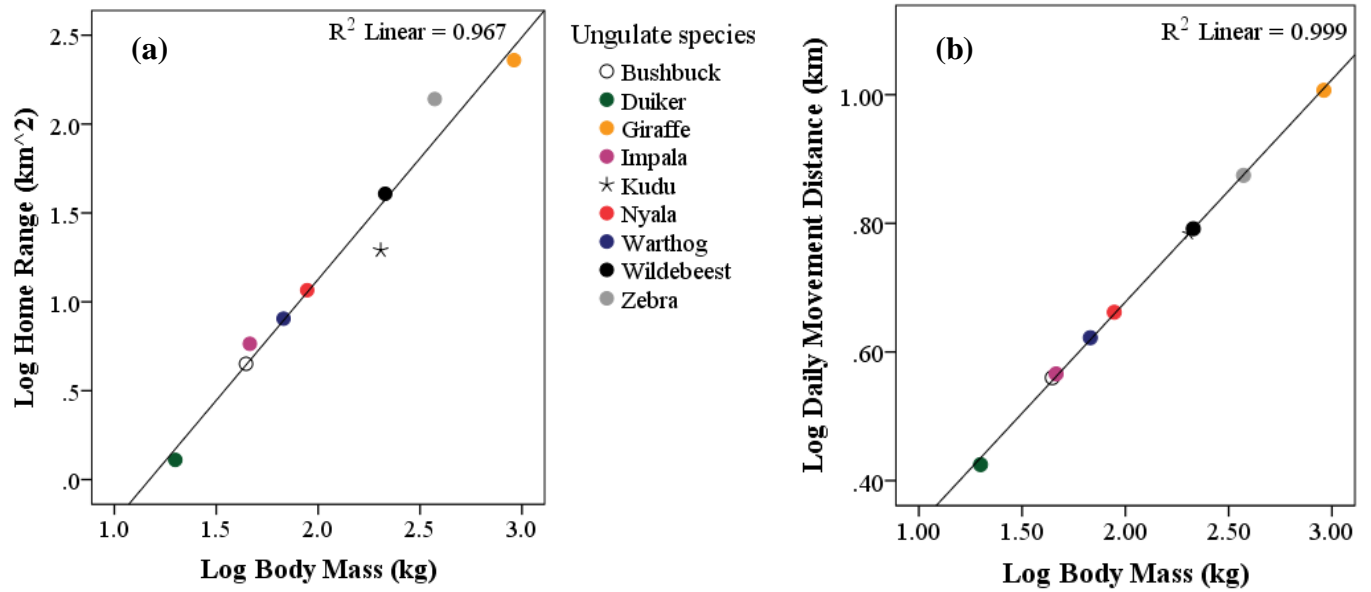


Figure 4.2. The \log_{10} plot relationship of home range (km²) ($R^2 = 0.967$; $y = 1.203 + 0.709x$) and daily movement distance (km) ($R^2 = 0.999$; $y = 0.041 + 2.890x$) with body mass (kg) of ungulate species.

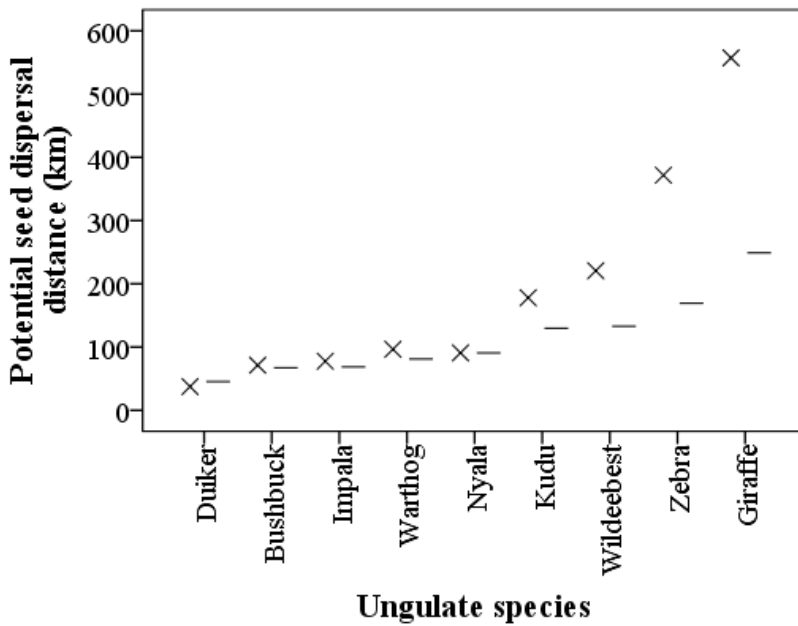


Figure 4.3. Potential seed dispersal distance by wild southern African ungulate species in the present study in KwaZulu-Natal, South Africa. Dispersal distance estimated using home range (km^2) (x) and daily movement distance (km) (–) as a distance factor.

4.5 Discussion

Movement patterns and distances of ungulate species are fundamental for seed dispersal of plant species (Nathan et al., 2008; Pellerin et al., 2016). Our present study demonstrated that the movement distances and spatial patterns of ungulates species are significant in understanding seed dispersal and contribute to further invasion of alien plant species. Our aim of the study was to quantify potential dispersal distances of ungulate species that interact with and those that ingest fleshy-fruited alien invasive plants. Although MRT (h) was not incorporated in the allometric equations for determining potential dispersal distances of ungulates, ungulates' gut physiology is a fundamental factor to consider in the ecology of seed dispersal. There was an expectation for smaller-bodied ungulates to have shorter retention times. However, a medium-bodied ungulate

(e.g. common warthog) and a large-bodied ungulate (e.g. zebra) had the lowest mean retention time. This may be influenced by their gut physiology, as allometric equations predict that non-ruminant ungulates experience shorter retention times, unlike the small-bodied ruminants (e.g. common duiker and impala). Considering this, an allometric scaling relationship between BM (kg) (Demment, 1983), MRT (h) (Demment & van Soest, 1985), implying that a longer DMD (km) by ungulates allows for longer retention time (Will & Tackenberg, 2008). In the case of seed dispersal, this allows for seeds to be dispersed over longer distances (Nathan, 2008; Bullock et al., 2011). In contrast, an empirical study by Picard et al. (2015), reported that a medium-bodied non-ruminant (wild boar, *Sus scrofa*) showed a longer retention time than a large-bodied ruminant ungulate (red deer, *Cervus elaphus*). When estimating retention time, we find separating ungulates and using allometric equations according to their digestive physiology to be suitable (Steuer et al., 2011). For example: in the study by Picard et al. (2015) retention time of wild boar was 36 h from empirically collected data. However, in our study, the theoretical retention time for common warthog was 32.33 h. The retention times for wild boar and common warthog were not varying from one another. We compare these two species as they are both within the Suidae family, therefore physiologically similar. Therefore, we consider the estimated MRT (h) of ungulate species to be most likely realistic, because of the equations being derived from empirical data.

The strong linear relationship of HR (km²) and DMD (km) with BM (kg) of ungulate species revealed that potential dispersal distances can be estimated using DMD (km) and HR (km²). The linear relationship showed daily distance travelled (km) and home range area (km²) of ungulate species is highly associated with their BM (kg), therefore influencing potential dispersal distances. A plethora of research has shown that body mass and home ranges are among the main variables influencing dispersal distances (Bowman et al., 2002; Sutherland et al., 2000; Santini et

al., 2013). Therefore, we estimated dispersal distances using HR (km^2) and DMD (km) as distance variables, based on an allometric equation (Santini et al., 2013). Dispersal distances based on HR (km^2) were modelled as the maximum potential dispersal distance (Santini et al., 2013), and we then manipulated the allometric equation to model dispersal distance using DMD (km). Both approaches showed varying dispersal distances of ungulates based on their BM (kg). Although there was little variation in dispersal distance for small ungulate species when compared using the two dispersal distance methods (HR, km^2 and DMD, km), significant differences were observed for larger ungulate species. Furthermore, we believe that the estimated dispersal distances based on DMD (km) are more likely to be realistic than those estimated based on HR (km^2). According to Santini et al. (2013) an increase in home range size of terrestrial mammals results in inaccurate estimation of dispersal distances. Perhaps at larger BM (kg) the relationship between BM (kg) and HR (km^2) becomes explained by a power rather than a linear function. A study by Santini et al. (2013) suggested that the relationships of both BM (kg) and HR (km^2) are better explained by a logistic relationship than a linear model when describing dispersal distance (Santini et al., 2013).

Theoretically, the estimated dispersal distances are most likely to be achieved by ungulate species. However, they may be limited by fencing around nature reserves and game lodges, therefore restricting ungulate movement and inevitably their dispersal distances. Habitat fragmentation, such as boundary establishment, may restrict movement distances and thereby dispersal distances by seed vectors (Slater & du Toit, 2002; Nathan et al., 2008). Therefore, permitting localised short dispersal distances (Santini et al., 2013). Nevertheless, their longer seed retention time (Cosyns et al., 2005; Mouissie et al., 2005; Seefeldt et al., 2010; Picard et al., 2015) and larger home range (Will & Tackenberg, 2008; Picard & Baltzinger, 2012; Picard et al., 2016)

permits for long-distance seed dispersal (Malo et al., 2000), therefore dispersing seeds at a regional spatial scale (du Toit & Cumming, 1999; Milton & Dean, 2001).

4.6 Conclusions

The main aim of our present study was to determine potential MRT (h) and dispersal distances (km) of wild southern African ungulate species observed ingesting fleshy-fruited alien invasive *L. camara*, *S. mauritianum*, and *O. monacantha* (as per Chapter 2), and of ungulate species where seeds of these alien plants were found (as per Chapter 3). In allometric equations, parameters such as body mass (kg), home range size (km²) and daily movement distance (km) were used to estimate MRT (h) and dispersal distances (km). MRT (kg) varied among ungulate species, firstly based on digestive physiology and then based on BM (kg). Hind-gut fermenters with larger body masses had shorter retention times than some small ruminant ungulates. Considering that MRT (h) of ungulate species are rare in the literature and not well represented, the present study prompts the need for additional research. Furthermore, dispersal distances (km) varied among ungulates, with the HR (km²) factor estimating longer dispersal distances than the DMD (km) factor. Though theoretically estimated, we find the MRT (kg) and dispersal distances (km) to be most likely realistic estimations since the allometric equations used were derived from empirical data. Because no allometric equation was found that included MRT (h) as a function of gut physiology when estimating dispersal distances (km) of ungulate species, we recommend that this be considered in future research. In conclusion, understanding dispersal distances of frugivorous species that consume fruits of alien invasive plants are fundamental for conservation purposes, as their dispersal distances may be used as a predictive tool for future alien invasions, allowing for proactive alien invasive plant management.

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4.9 Supplementary information

Supplementary information Table S4.1. Ungulate species characteristics used to estimate retention time and dispersal distances.

Calculated variables are shown as body mass (BM in kg), mean retention time (MRT in h), home range (HR in km²) and daily movement distance (DMD in km). Ungulate species are classified in their feeding type and digestive physiology, according to Estes (1991) and Hoffman (1989). Data represented as * was obtained allometrically using equations.

Ungulate Species	Feeding type	Digestive physiology	BM (kg)	MRT (h)*	HR (km ²)	DMD (km)*
Zebra, <i>Equus quagga</i>	Roughage grazer	Hindgut fermenter	373.19	32.89	138.43	7.49
Impala, <i>Aepyceros melampus</i>	Intermediate mixed feeder	Ruminant	46.16	46.09	5.81	3.68
Greater kudu, <i>Tragelaphus strepsiceros</i>	Selective concentrate browser	Ruminant	202.58	55.04	19.50	6.08
Giraffe, <i>Giraffa camelopardalis</i>	Selective concentrate browser	Ruminant	913.92	65.94	228.76	10.16
Nyala, <i>Tragelaphus angasii</i>	Intermediate mixed feeder	Ruminant	88.3	49.82	11.63*	4.59
Bushbuck, <i>Tragelaphus sylvaticus</i>	Selective concentrate browser	Ruminant	44.25	45.86	4.48*	3.63
Common warthog, <i>Phacochoerus africanus</i>	Roughage grazer	Hindgut fermenter	67.63	32.33	8.05*	4.19
Blue wildebeest, <i>Connochaetes taurinus</i>	Roughage grazer	Ruminant	213.22	55.38	40.56	6.19
Common duiker, <i>Sylvicapra grimmia</i>	Concentrate browser	Ruminant	17.9	41.14	1.29*	2.66

Additional data obtained from published literature (Smuts, 1975; Murray, 1982; du Toit, 1990; Bisset, 2004; Radloff & du Toit, 2004; Skinner & Chimimba, 2005; Fennesy, 2009; Bradley, 2012; Bartlam-Brooks et al., 2013; Kingdon & Hoffmann, 2013), van der Plas & Olff, 2014; Deacon, 2015; Kingdon, 2015; McQualter et al., 2015; Swanepoel et al., 2016; Deacon & Smit, 2017; Selebatso et al., 2017; Veldhuis et al., 2017 and Hewlett et al., 2020)

CHAPTER 5

Conclusions and recommendations

5.1 Introduction

Globally, the infestation of alien invasive plants in native plant communities incurs major problematic impacts on biodiversity and ecosystem functioning (Dutta, 2018). In addition to ecological impacts, alien invasive plants severely affect economies and societal well-being and livelihoods (Davies et al., 2016; Bitani et al., 2020). About 7% of South Africa's ecosystems are severely invaded by alien invasive plants (van Wilgen, 2018), requiring a comprehensive understanding of the dispersal pathways of alien plant invasion for effective management and control initiatives. Because fleshy-fruited invasive plants offer a higher nutritional reward than native species, frugivores gravitated towards these invasive plants, eventually forming part of native dispersal networks (Ramaswami et al., 2016). Thus, a mutualistic relationship is established (Wilson and Downs, 2012; Zungu and Downs, 2017). Ungulate species are among keystone species responsible in the functioning of terrestrial ecosystems (Picard et al., 2015) by the facilitation of seed dispersal (Baltzinger et al., 2019). Seeds are potentially dispersed via the gut of ungulates and seed deposited elsewhere for possible seed establishment (Schupp et al., 2017). However, ungulate species are equally considered to be potential dispersers of alien invasive plants (Baltzinger et al., 2019). The present research aimed to quantify ungulate-mediated seed dispersal of fleshy-fruited alien invasive *Lantana camara*, *Solanum mauritianum*, *Melia azedarach* and *Opuntia monacantha* by wild southern African ungulate species. The objectives were to: (1) determine visitation and fruit consumption of ungulate species with fleshy-fruited alien invasive plants; (2) assess the faecal contents of ungulate species to determine seeds of alien invasive plants

potentially dispersed; and (3) estimate potential seed dispersal distances of the invasive plants by wild southern African ungulates.

5.2 Visitation and fruit consumption of fleshy-fruited alien invasive plants by ungulates

The initial vital step in assuring the effectiveness of dispersal by frugivores is determined by factors such as the frequency and intensity of frugivory interaction (Prasad et al., 2010; Schupp et al., 2017). This is determined by the number of animal visitations to fruit plants and fruit consumption (Campos et al., 2018). The ingestion of fruits assures their dispersal to vacant habitats for potential population establishment (Baltzinger et al., 2019). Fleshy-fruited invasive plants increase their invasiveness fitness by establishing mutualistic relationships with seed vectors (Jordaan and Downs, 2012a, 2012b). Ungulate species are among underestimated seed vectors; therefore, a comprehensive understanding of their contribution to the seed dispersal of alien invasive plant species is imperative. Through a camera-trapping survey, a community of ungulate species were observed visiting fleshy-fruited alien invasive *L. camara*, *S. mauritianum*, and *O. monacantha* and ingesting fruits of *L. camara* and *O. monacantha* (Chapter 2). No data were captured for both animal visitation and fruit consumption of *M. azedarach* (Chapter 2). Greater visitations and fruit removal of the alien invasive plants were captured for giraffe *Giraffa camelopardalis* and bushbuck *Tragelaphus sylvaticus* for *L. camara*, impala *Aepyceros melampus* and greater kudu *Tragelaphus strepsiceros* for *O. monacantha* (Chapter 2). Our camera-trapping survey showed frugivory interactions between ungulates and alien invasive plants. Our study provides an increased understanding of their potential contribution to invasive plant species' dispersal dynamics in African savannahs (Chapter 2).

5.3 Seed composition of fleshy-fruited alien invasive plants in the dung of ungulate species

Habitats mostly preferred by frugivorous species receive the largest proportion of viable seeds after defecation (Picard et al., 2016). However, with the ingestion and dispersal of invasive alien plants, these preferable habitats become vulnerable to alien plant invasion (Cosyns et al., 2005). Moreover, defecated seeds persist in the seed banks, resulting in high survival rates and invasion capacity (Thompson et al., 1993). We used a dung deposition survey to predict microhabitats most likely vulnerable to alien plant invasion (Chapter 3). We also sought to understand the seed prevalence of the fleshy-fruited invasive plants in dung piles of ungulate species. Dung deposition counts varied among ungulate species, with impala and bushbuck the most common, and the common duiker *Sylvicapra grimmia* and zebra *Equus quagga* the least common (Chapter 3). Also, dung deposition varied among microhabitats, with savannah microhabitat receiving the highest deposition (Chapter 3). The prevalence of seeds of fleshy-fruited invasive alien plant species in dung piles of ungulate species varied significantly, with greater kudu *T. strepsiceros*, nyala *T. angasii* and bushbuck faecal containing the highest number of seeds. The lowest number of seeds per dung pile were for common warthog *Phacochoerus africanus* and common duiker (Chapter 3). No seeds of fleshy-fruited alien invasive plants were found in the dung of zebra. The seed prevalence fleshy-fruited invasive alien plant species varied per dung pile significantly in the various microhabitats, with the savannah microhabitat observed to receive the highest seed deposition (Chapter 3). The seed composition of alien invasive plants varied significantly, with higher numbers of *S. mauritianum* seeds per dung pile, compared with seeds of *L. camara* and *O. monacantha*. No seeds of *M. azedarach* were found in the dung pile (Chapter 3). Seed deposition per dung pile varied among sites, with Zingela and NLNP receiving the highest seed deposition. The savannah is most likely prone to alien plant invasion, as it received the highest number of

dung and seed deposition per dung pile. Though dung count surveys are useful for detecting elusive species, dung decay and dung sample exclusion serve as challenges when using this method. Importantly, our study provided foundational information necessary for predicting habitats prone to future alien plant invasion (Chapter 3).

5.4 Potential retention times and dispersal distances of alien invasive plants by ungulates

The determinants of where seeds are deposited are highly influenced by animal movement (both home range size and daily travelled distances) (Nathan et al., 2003) and retention of seeds in the gastrointestinal tracts (guts) of seed vectors (Picard et al., 2015). Additional factors include seed vector physiological characteristics such as body mass and digestive gut morphology (Clauss et al., 2008). In Chapter 4, we estimated the mean retention time (h) and dispersal distance (km) of ungulate species using allometric scaling equations (Santini et al., 2013). The ungulate characteristics considered were body mass (kg), home range size (km²) and daily movement distance (km). Mean retention time differed among ungulate species, primarily because of gut physiology. Hind-gut fermenters exhibited shorter retention times than ruminant species, irrespective of their body mass being greater than some ruminants. Dispersal distances varied among ungulate species. When using HR (km²) and DMD (km) as distance factors, potential dispersal distances were estimated to range between 37.45 – 557.22 km and 45.52 – 248.98 km, respectively (Chapter 4). Small-bodied ungulates exhibited shorter dispersal distances than large-bodied ungulates. When estimating dispersal distances of ungulate species, allometric equations that include mean retention time as a function of gut physiology are fundamental. Estimating mean retention time and dispersal distances of ungulate species are essential for employing appropriate management decisions for conservation purposes (Chapter 4).

5.5 Conclusions and recommendations

The present research aimed to evaluate ungulate-mediated seed dispersal, particularly the role of wild southern African ungulates in the dispersal of seeds of fleshy-fruited alien invasive *L. camara*, *S. mauritianum*, *M. azedarach* and *O. monacantha*. The results obtained from this study provide an understanding of the frugivory interactions of ungulate species and the fleshy-fruited alien invasive plants. This will assist in understanding ungulate species ingesting and possibly dispersing seeds of the invasive plants. Furthermore, dung deposition and seed deposition outcomes provide insight into seed persistence in the faecal droppings of ungulates and vulnerable microhabitats for potential plant invasion. Also, estimating mean retention time and dispersal distance is essential for understanding the extent to which alien invasive plants may be dispersed. Holistically, the findings provide insight into ungulate species' role in the dispersal of alien invasive plants. More research can still be conducted in assessing seed dispersal of fleshy-fruited alien invasive plants. Therefore we recommend the following: (1) a study based on direct observations on the interaction between ungulates and alien invasive plants to be able to quantify the disperser effectiveness of different ungulate species, which is important for a more accurate understanding of the potential role they play in the spread of invasive alien plants; (2) a study of a community-wide level of frugivorous species responsible of effectively dispersing the seeds of the fleshy-fruited alien invasive plants, as it is crucial to understand animal-mediated dispersal pathways; and (3) a seed deposition survey over consecutive sampling periods to determine temporal and spatial variations in seed deposition of fleshy-fruited alien invasive plants.

5.6 References

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