

**Fleshy-fruited invasive plant species in KwaZulu-Natal,
South Africa: Native avian seed dispersal and impact
assessment**

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ABSTRACT

Globally, alien plant species have been recognised as a major threat to biodiversity. The increased global trade and travel have resulted in the increased introduction of new species. Direct or indirect introductions of alien invasive plant species result in altered ecosystem functioning, negatively affect economies, human health and wellbeing. In forest systems, habitat fragmentation has major impacts on biodiversity including the facilitation of alien invasions. Habitat alteration creates disturbance zones that are associated with increased invasion success. South Africa, like other parts of the world, is severely affected by alien plant species. Fleshy-fruited invasive species are amongst the most damaging invasive species with major environmental, social and economic impacts. Fleshy-fruited invasive plant species integrate into local seed dispersal networks and form mutual relationships with local avian seed dispersers leading to increased invasion potential. The success of avian mediated seed dispersal is influenced by the functional traits of both the plant and avian seed dispersers. Considering the negative impacts of fleshy-fruited alien invasive species it is important to understand ecological processes leading to their successful spread and if high priority species are being targeted for management to guide policy and conservation. Understanding avian mediated dispersal is important as it gives insights into the species that could promote alien plant invasion. The aim of the present study was to assess avian seed dispersal, and ecological and socio-economic impacts of fleshy-fruited alien invasive plant species. The objectives were to (1) predict avian seed dispersers of fleshy-fruited alien invasive plant species; (2) determine the assemblage of native avian species potentially dispersing the seeds of *Lantana camara*; and (3) determine the socio-economic and ecological impacts of fleshy-fruited alien invasive plant species.

Firstly, we predicted the avian seed dispersers of fleshy-fruited invasive plant species in the Indian Coastal Belt Forest of KwaZulu-Natal Province, South Africa using functional

traits of avian species (body mass, gape width, bill length, degree of frugivory, foraging strategy, abundance and habitat specificity) and fleshy-fruited invasive plants (crop size, fruit size, seed size, number of seeds, plant height, plant habitat, fruiting period and derived invasiveness score). The results showed that small, abundant forest generalist avian species were potentially effective dispersers of fleshy-fruited invasive species. Fleshy-fruited invasive plant species that were more likely to persist in the disturbed Indian Coastal Belt Forest through avian-mediated seed dispersal were small-seeded, open habitat plants with relatively longer fruiting duration.

Secondly, we assessed the role of native avian species in the potential dispersal of a highly invasive shrub *Lantana camara* of the family Verbenaceae in Pietermaritzburg, KwaZulu-Natal, South Africa. Avian species visiting *L. camara* were observed and potential dispersal distances estimated. The results showed that native avian species were potential seed dispersers of *L. camara* were mostly relatively small, moderately frugivorous avian species. The dark-capped bulbul (*Pycnonotus tricolor*) showed relatively high visitation frequencies to *L. camara* and was more likely the main effective dispersers of the plant. Potential seed dispersal distances were shown to range from 9 to 45 km and long distance seed dispersal distances were shown to be rare and only limited by rarely large avian frugivores.

Lastly, we assessed the ecological and socio-economic impacts of fleshy-fruited invasive species using the generic impact scoring system. The results showed that fleshy-fruited invasive plant species have both socio-economic and environmental impacts. The highest environmental impacts were shown to be on ecosystem and vegetation, or plant and the highest socioeconomic impacts were on agriculture, forest production and human health.

The results presented in this thesis provide essential insights into the importance of avian mediated seed dispersal in the invasion of fleshy-fruited invasive plant species. The

findings of the study also highlight the importance of predictive approaches in informing the management of invasions and showed fleshy-fruited invasive plant species with high socio-economic and ecological impacts. Knowledge of species with high impacts will help in guiding resource allocation and preventing the introduction of high-risk species. Also, ecologists and other decision-makers should consider ecological processes that are leading to the spread of invasive plant species in management practices or plans.

PREFACE

The data described in this thesis were collected in Pietermaritzburg, KwaZulu-Natal, Republic of South Africa from April 2017 to May 2018. Experimental work was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Professor Colleen T. Downs.

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.



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Nasiphi Bitani

November 2019

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



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Professor Colleen T. Downs

Supervisor

November 2019

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DECLARATION 1 - PLAGIARISM

I, Nasiphi Bitani, declare that

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2. This thesis has not been submitted for any degree or examination at any other university.
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**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

N Bitani, DA Ehlers Smith, YC Ehlers Smith & CT Downs

Predicting avian dispersers of fleshy-fruited invasive plant species from bird and plant functional traits

Author contributions:

NB conceived paper with DAE, YCE and CTD. NB collected and analysed data and wrote the paper. DAE, YEC and CTD contributed valuable comments to the manuscript.

Publication 2

N Bitani & CT Downs

Potential dispersal of invasive *Lantana camara* by native bird species in KwaZulu-Natal, South Africa

Author contributions:

NB conceived paper with CTD. NB collected and analysed data and wrote the paper. CTD contributed valuable comments to the manuscript.

Publication 3

N Bitani, TC Shivambu, N Shivambu & CT Downs

A global impact assessment of alien invasive fleshy-fruited plants dispersed by avian species in South Africa

Author contributions:

NB conceived paper with TCS, NS and CTD. NB collected and analysed data and wrote the paper. TCS, NS and CTD contributed valuable comments to the manuscript.

A handwritten signature in dark ink, appearing to read 'NB' followed by a stylized flourish.

Signed:

Nasiphi Bitani

November 2019

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“And we know that all things work together for good to them that love God, to them who are the called according to his purpose.” (Romans 8: 28)

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CHAPTER 1

Introduction

Alien invasive species are defined as species that are successful outside their native range (Jordaan et al., 2011; Burns et al., 2019) and they are rated as the second major threat to the biodiversity after habitat destruction effects on the natural environment (Jordaan et al., 2011; Nentwig et al., 2016; Ruwanza and Shackleton, 2016). Alien species invasion is recognised as a component of global change (Bacher et al., 2018; Meyerson et al., 2019; Shackleton et al., 2019) with impacts across all ecosystems in the world (Carrion-Tacuri et al., 2012; Davies et al., 2016) contributing to biodiversity loss, altering ecosystem functioning (French et al., 2014; Ramaswami et al., 2016) negatively affecting economies (Jordaan and Downs, 2012; Vardien et al., 2012; Ruwanza and Shackleton, 2016; Frost et al., 2019), human health and wellbeing (Jordaan et al., 2011; Booth, 2014; Ruwanza and Shackleton, 2016; Frost et al., 2019). Different habitats vary in their susceptibility to invasion and the major influence is the level of disturbance (Vardien et al., 2012) and the availability of resources (Pysek and Richardson, 2010). Habitats that are more frequently disturbed (e.g habitats that are subjected to human activities) are more susceptible to invasions than less disturbed habitats. Interest in invasion research has grown over the years and it has been motivated by conservation concerns and the problems that arise as a result of the new introductions of invasive species. The main goal in invasion science includes understanding how new habitats are invaded, impacts associated with invasive species (Bartz and Kowarik, 2019), if the range of species will increase (Bonilla and Pringle, 2015) better management strategies for newly introduced and well-established invasive species (Davies et al., 2016; Shackleton et al., 2019). Worldwide conservation ecologists are faced with a major challenge of controlling alien invasive species (i.e. newly introduced and well-established species), preventing the damage they cause to the natural ecosystems and repairing systems that have already been damaged (Richardson and van

Wilgen, 2004; Davies et al., 2016). The geographical extent of alien invasive species is continually increasing influenced by the increased global trade and travel and human populations and natural systems are strongly affected by these changes (Cardeccia et al., 2018; Cope et al., 2019).

1.1 Alien invasive plants in South Africa

South Africa's natural systems are under serious threat of invasive species as invasive species with both economic and ecological impacts have been reported to be increasing (Nel et al., 2004; Rouget et al., 2004; Davies et al., 2016; Henderson and Wilson, 2017; van Wilgen, 2018; Wilson et al., 2018). Of all the countries in the world, South Africa has the most problems relating to alien plant invasions (Richardson and van Wilgen, 2004; Wilson et al., 2018; Bennett and van Sittert, 2019) and many of these invasive species are well established while some are still at early invasion stages (Nel et al., 2004; Baard and Kraaij, 2019). Alien plant species are the most widespread and damaging of invasives in the country and have been reported to cover approximately 7% of the country (van Wilgen, 2018).

In South Africa there has long been the awareness of the issues regarding alien invasive species and this knowledge can be dated back to the 1800s but the first policy addressing the issue of alien invasive plants was around only around the 1980s (Richardson and van Wilgen, 2004). It is important that the contributions of local researchers and conservation bodies to understanding alien invasions in South Africa species are acknowledged. Research on alien plant invasion has been a concern and explored in South Africa but most have been mainly focused on management. For example, the Working for Water programme that started in 1995 presents the initiation significant stage aimed to come up with management practices for alien invasive throughout South Africa (Richardson and van Wilgen, 2004, Rouget et al., 2004). The South African government has invested over 7 545 100 000,00 ZAR through the Working for

Water programme to manage alien invasive species especially trees (Bennett and van Sittert, 2019). The limited funds are contributing to ineffective management thus the problem is escalating (Nel et al., 2004; van Wilgen, 2018). Therefore, improved understanding of processes that are leading to the continuous spread of invasives is important for effective management. Also, South African research on alien invasive plant species has placed more focus on the fynbos biome because well-documented invasions are along with the western and eastern coastal areas of the country (Carruthers et al., 2011). Clusella-Trullas and Garcia (2017) argued that the selection of study areas is influenced by the accessibility, the research interests of research institutions and biological invasion researchers.

1.2 Impact assessment

Invasive species pose a threat to the introduced environments but not all impacts are unacceptable (Bartz and Kowarik, 2019; Padayachee et al., 2019). Also, impacts associated with invasives vary across different habitats and taxa groups (Hawkins et al., 2015; Bacher et al., 2018) but are mainly associated with changes to the natural environments, society and economy (Measey et al., 2016; Kumschick et al., 2017). Consequently, impacts associated with biological invasions have led to the development of impact assessment tools with the aim to quantify impacts posed by alien invasive species (Nentwig et al., 2016; Rumlerova et al., 2016; Bartz and Kowarik, 2019). These tools provide an alternative to the listing of species based on expert knowledge that is often subjective (Vaes-Petignat and Nentwig, 2014). The impact assessment tools are based on scientific evidence (Kumschick et al., 2015; Moshobane et al., 2019) and are comparable across different regions and taxa (Nentwig et al., 2016). The impact quantifying approaches give insights to which species are detrimental so that management prioritise those species with major impacts (Rumlerova et al., 2016; Kumschick et al., 2017; Jubase et al., 2019) and inform decisions relating to the introduction of species (Bartz and

Kowarik, 2019). Bacher et al. (2018) argued that in as much as progress has been made to quantify impacts of invasive species, more focus has been placed on ecological impacts. This highlights the importance of assessment studies that aim to integrate both ecological and social related impacts. Despite the challenges associated with risk impact assessment tools it is important that the listing is compiled to guide management and prohibit the introduction of species with high impacts (Moshobane et al., 2019). In South Africa, knowledge, if species with high impacts species are prioritised for management, is limited (Moshobane et al., 2019) as a comprehensive quantitative assessment of alien invasive plants is lacking. Therefore, studies assessing the impacts are important to guide the allocation of limited resources.

1.3 Seed dispersal

Plant reproduction in many habitats is dominated by the interaction between fruit and their seeds and animals (Armesto and Rozzi, 1989; Dennis, 2007; Bonilla and Pringle, 2015) and these interactions influence the functioning and structure of ecosystems (Schleuning et al. 2015). Ecologists have long been fascinated by animal-fruit interactions and the interest in early plant-animal studies was focused on islands that have been mainly on food choice, foraging behaviour and nutrients (e.g Dennis, 2007). Seed dispersal is defined as the movement of seeds from the parent plant and is associated with the increased seedling establishment (Munoz et al., 2016). This process begins when frugivorous species interact with the fruit of a plant and form mutual relationships (Armesto and Rozzi, 1989; Gosper et al., 2005) and is regarded as an ecosystem service as people can directly or indirectly benefit from it (Schleuning et al., 2015). Seed dispersal is important for gene flow (Schupp et al., 2010; Milotic and Hoffman 2016; Weighill et al., 2017; Johnson et al., 2019) maintaining plant communities (Rey and Alcantara, 2000; Spiegel and Nathan, 2007; Weir and Corlett, 2007; Thomson et al., 2011; Wilson and Downs, 2012), colonisation of new sites (Russo et al., 2006),

alien invasion (Buckley et al., 2006; Schupp et al., 2010; Ramaswami et al., 2016; Zwolak, 2018; Yoshiwaka et al., 2019) and have important management implications (Spiegel and Nathan, 2007; Aslan, 2011; Bonilla and Pringle, 2015). The main environmental benefits of frugivore mediated seed dispersal is deposition of seeds to favourable microsites, escaping predation closer to the parent plant (Martin-Albarracin et al., 2018; Rehm et al., 2019) and reduced competition from both parent plant and siblings (Herrera et al., 1984; Milotic and Hoffman, 2016; Zwolak, 2018).

Quantifying animal-plant interactions is relatively complex (Yoshiwaka et al., 2019) as a result of unpredictable frugivore behaviour (Kleyheeg et al., 2017; Zwolak, 2018) and often involves multiple animal and plant species (Gonzalez-Castro et al., 2015). The scientific literature on seed dispersal has grown driven by the importance of this process in plant regeneration (Dennis, 2007; Schupp et al., 2010), the fitness of individual plant species (Vidal et al., 2013; Johnson et al., 2019) maintenance of genetic diversity (Soons et al., 2016) and ecological functioning (Dugger et al., 2018). Woody plant species in the tropics and subtropics rely on vertebrates for dispersal (Armesto and Rozzi, 1989; Voigt et al., 2011) and about 90% tree species are dependent on frugivores for seed dispersal (Dugger et al., 2018). Fleshy-fruited plant species are dependent on animal-plant interaction for the movement of their seeds (Munoz et al., 2016). Therefore, frugivorous species are important in shaping vegetation dynamics (Weighill et al., 2017) and influencing the spatial distribution of plant species in the landscape (Russo et al., 2004; Zwolak, 2018). Seed dispersal research has mainly focused on the importance of plant-animal interaction in forest systems regeneration (e.g. de Assis Bomfim et al., 2018; Rehm et al., 2018) and understanding of plant-animal interaction in facilitating alien plant invasion have grown extensively with the exception of Africa and southern Africa in particular where there have been fewer studies.

little has been done evaluating the importance of animal-plant interactions in facilitating invasion by fleshy-fruited invasive species.

1.4 Dispersal effectiveness

Effectiveness is a broad concept that varies across studies, for seed dispersers effectiveness relates to the successful establishment of dispersed seeds (Schupp et al., 2010; Schupp et al., 2017). Effectiveness of frugivores in the seed dispersal of a species is determined by the contribution frugivores make to the plant fitness of a species (Whitney et al., 1998) and seeds are effectively dispersed if they are deposited away from parent plants in low densities (Stevenson, 2000). Dispersal effectiveness is determined by the quantity and quality of the dispersal service provided (Whitney et al., 1998; Mokotjomela et al., 2015; Fontúrbel et al., 2017; Martin-Albarracin et al., 2018; Naniwadekar et al., 2019) and the traits of frugivores influences the quality and quantity of dispersal (Buckley et al., 2006; Spiegel and Nathan, 2007). Fruit size, competition, number of dispersers and visits (Graham, 1995; Buckley et al., 2006; Mokotjomela et al., 2015; Fontúrbel et al., 2017), number of seeds that are dispersed per visit (Whitney et al., 1998; Spiegel and Nathan, 2007; Schupp et al., 2010; Mokotjomela et al., 2015; Fontúrbel et al., 2017; Martin-Albarracin et al., 2018; Naniwadekar et al., 2019) and the duration of visits (Stevenson, 2000) are amongst the factors that dispersal quantity is dependent on. Quality is the treatment of the seeds in the mouth and gut of the avian species and is determined by the amount of time seeds are retained within the gut system of an invader, movement patterns of dispersers (Whitney et al., 1998; Schupp et al., 2010), germination and seedling survival (Fontúrbel et al., 2017) and type of sites seeds are deposited (Stevenson, 2000; Naniwadekar et al., 2019). Quality is also influenced by how seeds are treated by the seed dispersal agent. Mokotjomela et al. (2015) stated that dispersal effectiveness is affected by quantity rather than quality. Determining the probability of seed survival where they are

deposited is the most challenging seed effectiveness factor because of the large temporal scales for determining seed fate. Effectiveness of disperses can be determined by observations at fruiting plants and germination trials of seeds that have been ingested by frugivores (Whitney et al., 1998). Fontúrbel et al. (2017) argued that most seed vectors are not effective dispersers as they often provide poor quality interactions (e.g few visits, seed damage, deposition to unfavourable sites. Most studies on avian mediated dispersal have overlooked the importance of plants in promoting the success of their dispersers and have mainly focused on the contribution of dispersers to the fitness of plant species.

1.5 Seed dispersal of fleshy-fruited invasive plant species

The availability of dispersers is the most important factor in successful invasion (Buckley et al., 2006; Saavreda et al., 2017). Native generalist frugivores play a key role in the dispersal of many fleshy-fruited invasive plant species to different locations (Panetta and McKee, 1997; Buckley et al., 2006; Martin-Albarracin et al., 2018) and often have a profound impact on the invasion dynamics through dispersal services. One of the key strategies for invasive plant species to be successful is to integrate into local existing ecosystems by being part of dispersal mutualisms (Alan, 2011; Voigt et al., 2011; Ramaswami et al., 2016; Martin-Albarracin et al., 2018). Mutual relationships can be either when native dispersers shift their foraging patterns to use the fruits of an invasive plant or when plants reunite with its disperser species from their native range (Gosper et al., 2005; Alan, 2011). Mutualism facilitates many plant invasions as dispersers gain a food source and invasive plant seeds are dispersed increasing invasion success (Gosper et al., 2005; Ramaswami et al., 2016). The likelihood of incorporating a new fruit source by native avian species is likely as seed dispersal networks are rarely specialised (Ramaswami et al., 2016) fleshy-fruited invasive species produce large crop sizes fruits out of the fruiting season of natives (Martin-Albarracin et al., 2018), and higher nutritional content

(Ramaswami et al., 2016). Despite studies showing the importance of animal-plant interaction in the success of fleshy-fruited invasive species, the influence of such interaction ineffective management of invasive species remains largely unexplored. To effectively manage well established invasive species that have formed dispersal networks with native dispersers it is important to understand which avian species are contributing to their successful establishment.

1.6 Avian mediated seed dispersal

Amongst other effective seed vectors like mammal species (Jordaan et al. 2012), birds are important seed vectors for fleshy-fruited plants worldwide (Graham, 1995; Fleming and Kress, 2011; MacFarlane et al., 2016; Wyman and Kelly, 2017; Bartel et al., 2018), because they are the most abundant and competent seed vectors (Naranjo et al., 2003; Viana et al., 2016). Mokotjomela et al. (2013a; b) stated that of 1340 angiosperm indigenous tree species in Southern Africa, 23% are dispersed by birds. Birds disperse seeds through endozoochory (i.e. seed ingestion) or epizoochory (e.g attachment of seeds in the feathers or legs) (Nathan et al., 2008; Viana et al., 2016; Milotic and Hoffman, 2016). Fleming and Kress (2011) stated that birds have contributed a lot to the dispersal of fruit-bearing plants because of their abundance, diversity, range sizes and the frugivory distributed throughout their phylogeny.

Mutualistic relationships between invasive species with fleshy fruits and native bird species have been recognised (Jordaan et al., 2011; Mokotjomela et al., 2013a) and native bird species are thought to be the main disperser of many invasive plant species (Gooden et al., 2009; Carrion-Tacuri et al., 2012; Jordaan et al., 2011; Gosper et al., 2015; Mokotjomela et al., 2015). These mutualistic relationships have an effect on conservation concerns (Carrion-Tacuri et al., 2012) as birds are likely to increase the distribution and density of invaders by feeding on invasive plant species. Birds are generally attracted to fleshy fruit that are red or purple in colour, relatively small and lack physical seed protection (Whittaker and Jones, 1994). Fleshy

fruited invasive plants usually have these desirable traits that are attractive to avian species and unlikely to suffer from a lack of mutual relationships for dispersal services because of their fruit traits (Carrion- Tacuri et al., 2012). Due to these relationships, native plant communities are replaced by alien invasive plants as an available food source thus dominate (Jordaan et al., 2011). The contribution of birds to the success of invasive species remains unknown leading to ineffective management of alien invasive plant species (Gosper et al., 2005; Ramaswami et al., 2016). Bird movement patterns, avian foraging behaviour, diversity of the local avian assemblage, body size and seed retention time have implications on invasion success and dispersal services offered by different bird species (Gosper et al., 2005; Vidal et al., 2013; Saavedra et al., 2017). Avian mediated dispersal has been mostly studied to understand the importance of avian species in forest regeneration (e.g Gonzalez-Castro et al., 2019). Connecting isolated plant communities and knowledge of avian species that are effective dispersers of many invasive plant species remains relatively poorly studied.

1.7 Functional traits

The success of frugivore dispersed plants depends on the morphological traits of both the plant and animal species (Tiribelli et al., 2017). The traits of the species can either (i) promote animal-plant interaction if the traits link or (ii) results in non-interaction if there is a mismatch between the traits of the species and this is termed the forbidden link (Munoz et al., 2016). For example, it has been shown that if the gape width of the avian frugivore is smaller than the fruit size the frugivore will not be able to swallow the seed (Symes and Downs, 2001; Moran et al., 2004; Naniwadekar et al., 2019; Rehm et al., 2019). Animal traits that have been shown to influence the seed dispersal capacity of frugivorous species include movement patterns (Vidal et al., 2013; Rehm et al., 2019), bill size, wing morphology, avian body size (Mokotjomela et al., 2016; Pigot et al., 2016; Rehm et al., 2019), bird behaviour and gape width (Naniwadekar

et al., 2019). Plant species traits that have shown to influence seed dispersal are plant height, fruit size, plant crop size (Munoz et al., 2016). Crop size size influence visitation rates and the quantity of seeds that can be consumed, Despite the progress of studies evaluating important plant and animal traits in seed dispersal most seed dispersal studies have focused on the influence of gape width and seed size. Also, most studies evaluating the importance of functional traits in seed dispersal have mainly focused only on disperser traits and the relationship of most traits important for seed dispersal remains poorly understood. This highlights the importance of the need for understanding animal and plant traits that are important for avian mediated seed dispersal networks.

1.8 Dispersal distances of avian species

It is important to quantify seed dispersal distances as it helps in understanding plant dynamics in a landscape (Weir and Corlett, 2007; Jansen et al., 2008), biological invasion (Cain et al., 2000; Mokotjomela et al., 2015) and gives an insight of the contribution of different frugivorous birds to seed dispersal at different distances (Jordano et al., 2011). Quantifying seed dispersal distance is complex and the contribution of avian species to plant community patterns remains unclear (Rehm et al. 2019). Despite the difficulties of quantifying seed dispersal distances of avian species different techniques have been used to estimate seed dispersal distances distance. Approaches to determine seed dispersal distances include genetic (e.g Cain et al., 2000), seed distribution patterns (e.g Nathan and Muller-Landau, 2000) and modeling (e.g Levey et al., 2005; Rehm et al., 2019). The use of seed traps for determining seed dispersal distances is limited by the small fraction of the seed shadow that is sampled and rare long distances dispersal events are often not considered (Weir and Corlett 2007). Alternatively, technology has proven to be of good use in determining dispersal distance, for example, Weir and Corlett (2007) estimated dispersal distance in Hong Kong China using radio

transmitters. Similarly, Wotton and Kelly (2012) used radio transmitters to estimate avian seed dispersal distances of in New Zealand. The main challenge with using transmitters is that they are expensive and for relatively small birds (< 50g) it is challenging to get the proper sizes.

Models that have been used to quantify seed dispersal distances of avian species seed uses retention time, movement patterns and body size (e.g Nathan et al., 2008; Wotton and Kelly, 2012; Mokotjomela et al. 2015; Rehm et al., 2019). Body mass of frugivores determines the amount of seeds that can be retained within the gut system of frugivores (Buckley et al., 2006; Spiegel and Nathan, 2007; Vidal et al., 2013) and fruits that can be consumed per visit (Spiegel and Nathan, 2007). Different studies have shown that relatively larger avian species contribute to rare longer seed dispersal distances than relatively small species (Nathan et al., 2008; Mokotjomela et al. 2015; Rehm et al., 2019). Seed dispersal distances have been shown to be affected by seed retention time (time seeds are within the gut system of frugivores) (Stevenson, 2000; Buckley et al., 2006; Weir and Corlett, 2007; Rehm et al., 2019) and it is influenced by frugivore, seed type (Whittaker and Jones, 1994) and seed size (Stevenson, 2000).

Birds are the group of dispersers that have the potential to disperse seeds over greater distances especially migratory birds move seasonally overcoming geographical barriers and increase the probability of successful establishment as they move across habitats with similar characteristics (Nathan et al., 2008, Viana et al., 2016). The importance of migratory birds as dispersers is likely to be important in the temperate regions of the Northern Hemisphere as they occur in the high altitudes (Viana et al., 2016). In the tropical and subtropical regions, many birds' species have the potential to contribute to long seed dispersal as they travel long distances within a short period of time (Viana et al., 2016). This is true as (Mokotjomela et al., 2013a) showed a seed dispersal distance curve up to 400 km of three bird species and ranged from 9.4- 21.2 km when considering seed retention time and flight distance. The potential of

birds to contribute to long dispersal distances provide the basis for quantifying dispersal distances (Viana et al. 2016). Although progress has been made in quantifying seed dispersal most studies have focused on forest communities.

1.9 Recruitment patterns of dispersed seeds

Distribution of seeds is strongly influenced by frugivores, therefore plant-frugivore interactions have evolutionary and ecological consequences from population to community level (Vazques et al., 2009; Vidal et al., 2013). Seed dispersals plays an important role in determining the spatial structure of plant communities (Schupp, 1995; Willson, 1993; Rey and Alcantara, 2000; Fragoso and Huffman, 2000; Nathan and Muller-Landau, 2000; Russo et al., 2004; Tiffney, 2004; Spiegel and Nathan, 2007) and colonisation of potential recruitment sites invasion (Nathan and Muller-Landau, 2000; Fontúrbel et al., 2017). The results of recruitment are expressed by the entry and distribution of new individuals in a habitat (Ribbens et al., 1994; Rey and Alcantara, 2000) and depend on seed viability (Fontúrbel et al., 2017). Distribution patterns often vary and are dependent on different factors including the distance from the parent plant, different microsites, different times and plant species (Nathan and Muller-Landau, 2000). These differences are a result of a set of different processes that can operate over differences in range distance (Nathan and Muller-Landau, 2000; Russo et al., 2004). Therefore, the spatial pattern of plants that are dispersed by frugivores can be viewed as the balance between post dispersal and post dispersal processes (Russo et al., 2004; Weir and Corlett, 2007). The importance of dispersers on recruitment dynamics can be determined if seed dispersal is the only event leading to recruitment (Rey and Alcantara, 2000; Jordaan et al., 2011; Thabethe et al., 2015). It can be determined by evaluating the role of a disperser on recruitment success (Schupp et al., 2010). If the chances of a seed to be dispersed are lower than the chances of a dispersed seed to establish disperses are said to be limiting recruitment (Rey and Alcantara,

2000). However, this is unlikely for fleshy fruited plant species as they often produce fruit in great amounts that are dispersed by animals (Rey and Alcantara, 2000). This then leads to the hypothesis that dispersal cannot be the limiting process in the recruitment dynamics (Rey and Alcantara, 2000) hence this process shapes spatial recruitment patterns (Schupp, 1995). Most studies on dispersal patterns are in the forests and have mainly used seed traps or developed models of the behaviour of a frugivore (Russo et al., 2004). According to Schupp and Fuentes (1995), it is important to understand where in the landscape dispersed seeds arrive. Most literature on animal mediated dispersal of fleshy-fruited plants focuses on frugivory and less on the patterns of deposition (Schupp and Fuentes, 1995; Schupp et al., 2010).

1.10 Focus on the case study invasive plant species, *Lantana camara*

Lantana camara is a highly invasive shrub in the Verbenaceae family that is native to the tropical regions (Sanders, 1987; Scott et al., 1997; Yaradua and Shah, 2020). Due to the vigour of the plant management through the use of herbicides and burning is not viable (Scotts et al., 1997). The fruits of the *L. camara* plant have evolved more than once, therefore the plant is likely to be polyphyletic (Sanders, 1987). The taxonomy has been divided into four genera mainly based on the floral characteristics (De Sousa et al., 2018). However, this division is very difficult because of the variation in the flower colours and widespread hybridization (De Sousa et al., 2018). In the world, *L. camara* is listed in the top ten of invaders based on the number of countries the plant has invaded (Nanjappa et al., 2005; Bhagwat et al., 2012, Fig. 1.1). *Lantana camara* generally grows in small clumps in moist areas in its native range (Vardien et al., 2012). This invader was first introduced in 1858 in the Cape Town gardens and in 1883 in KwaZulu-Natal as an ornamental plant (Urban et al., 2011). India, South Africa, and Australia have been successfully invaded by *L. camara* (Nanjappa et al., 2005). It has been suggested that from the observed diversity of *L. camara* in South Africa that most likely other

introductions occurred and are not documented or the introduced one was genetically diverse (Vardien et al., 2012). The plant was then introduced as an ornamental plant to other provinces and survived as *L. camara* can tolerate different conditions. *Lantana camara* has prickles that discourage browsing and potentially contributed to it being persistent in newly invaded areas (Vardien et al., 2012). Frugivorous birds are likely to have dispersed seeds of *L. camara* over great distances as most damaging invasive species owe their successful establishment to frugivorous vertebrates (Jordaan et al., 2011; Urban et al., 2011). With the help of frugivores, this invader transforms indigenous vegetation into thickets of *Lantana* (Ramaswami et al., 2016). There is a gap in South African literature with regards to distances *L. camara* can be dispersed over, studies from other places have shown that the seeds can be dispersed to about 1 km (Vardien et al., 2012). Also, the assemblage of avian species that are dispersing the plant in the wild is not known (Taylor et al., 2018). Rivers have also been shown to play a major role in dispersal however in South Africa their contribution alone cannot be used to explain the present distribution of *L. camara* (Bhagwat et al., 2012). In South Africa this invader has invaded millions of hectares (Urban et al., 2011, Bhagwat et al., 2012; Ruwanza and Shackleton; 2016; Taylor et al., 2018) and has been reported to have both environmental and economic impacts (Urban et al., 2011; Vardien et al., 2012). Biodiversity loss, reducing the productivity of grazing land and poisoning cattle have been reported to be negative impacts of *L. camara* (Urban et al., 2011; Sampson et al., 2018). The reduction of productivity is costing South African farmers approximately ZAR 67 million per year (Urban et al., 2011). The effects of *L. camara* on biodiversity are limited but its effects on invertebrate's diversity, livestock and humans have been documented (Vardien et al., 2012). In Tanzania, this shrub hosts the tsetse fly, a vector for African sleeping sickness (Vardien et al., 2012). Ecological and diverse morphological characteristics have contributed to the success of *L. camara* (Urban et al., 2012). Over 50 varieties have been documented in South Africa alone (Vardien et al., 2012). In has

been reported that this invader has a broad ecological gradient, for example, it is present in seven out of nine biomes in the country (Vardien et al., 2012). *Lantana camara* produces large crop sizes that are available to a suit of dispersers (Carrion-Tacuri et al., 2012; Ramaswami et al., 2016) with approximately 12 000 fruits per tree (Jordaan et al., 2011). *Lantana camara* has been studied extensively because of its exceptional invasiveness, however most of the literature on this shrub is mainly on biological and none on the invasion dynamics. Hence, data on the main drivers that lead to the successful invasion of *L. camara* are lacking (Bhagwat et al., 2012). Efforts by government and non-governmental organisations to eradicate *L. camara* in South Africa started as early as in the 20th century (Bhagwat et al., 2012). The government spent 180.6 million ZAR between the years 1995 and 2008 trying to control *L. camara*. Despite the attempts to manage *L. camara*, this invasive shrub remains a concern in South Africa (Bhagwat et al., 2012). The invasion of *L. camara* can be better controlled by understanding the spread and dispersal patterns.

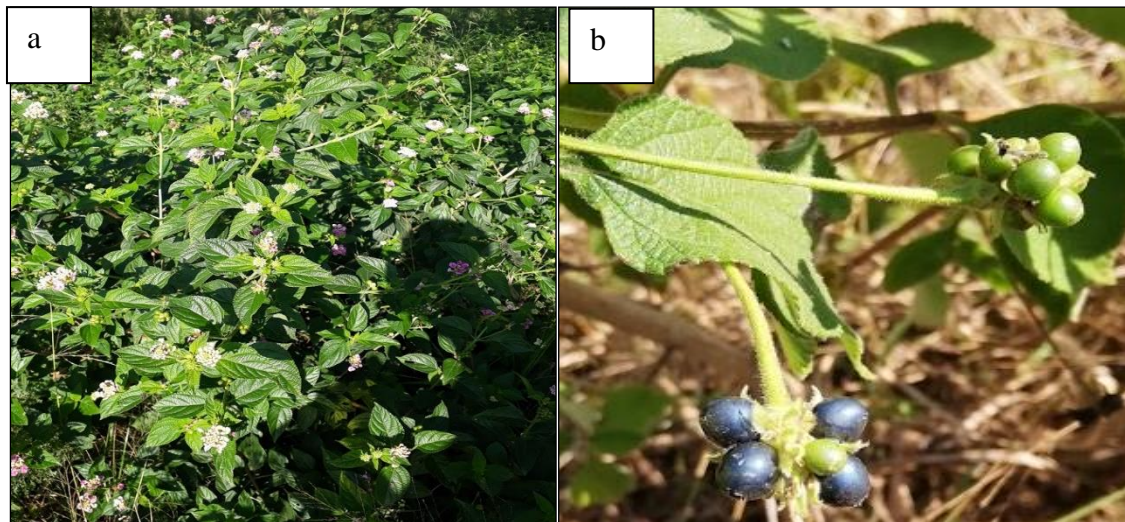


Fig 1.1. Photographs showing *Lantana camara* (a) infestation, and (b) ripe and unripe fruits.

1.11 Study area

The present study included three main sites in KwaZulu-Natal, South Africa (Fig. 1.2). The first site, Fountain Hill Estate, is a nature reserve and commercial farm located outside Wartburg, Pietermaritzburg. Fountain Hill Estate is approximately 3000 ha and the nature reserve is 1600 ha (Grey et al., 2009). The area receives rainfall during the summer months (October- February) averaged 694 mm annually (Chibarabada et al., 2018). The site has a minimum and maximum average temperature of 3 °C and 37°C, respectively (Musokwa et al., 2019). The second site, Ukulinga Research Farm, is located close to Pietermaritzburg (29° 39' 51" S, 30° 24' 13" E). The site is approximately 350 ha, dominated with grasses and *Vallechia* (*V. sieberiana*, *V. nilotica* and *V. Karoo*; previously known as *Acacia*) trees scattered around (Kirkman et al., 2014). The site receives seasonal rainfall and mostly during summer months with an annual precipitation average of 790 mm (Forrestel et al., 2014). The third site was a portion of the Indian Coastal Belt Forest (100 km × 27 km) in the southern coast of KwaZulu-Natal Province, between UMtamtamvuna Nature Reserve (31°04' 69" S, 30°11'39" E) Vernon Crookes Nature Reserve (30°16'17" S, 30° 36' 34" E; Ehlers Smith et al., 2017a, b). This site consists of two main habitat types the coastal scarp and coastal lowland forests (Ehlers Smith et al., 2017). This forest has been extensively fragmented owing to intensive agriculture (Ehlers Smith et al., 2017a, b) including commercial farming, sugarcane (*Saccharum officinarum*), banana (*Musa* spp.) and macadamia nut (*Macadamia integrifolia*) (Ehlers Smith et al., 2017b). The site receives seasonal rainfall and is mostly during the summer months (Ehlers Smith et al., 2017c).

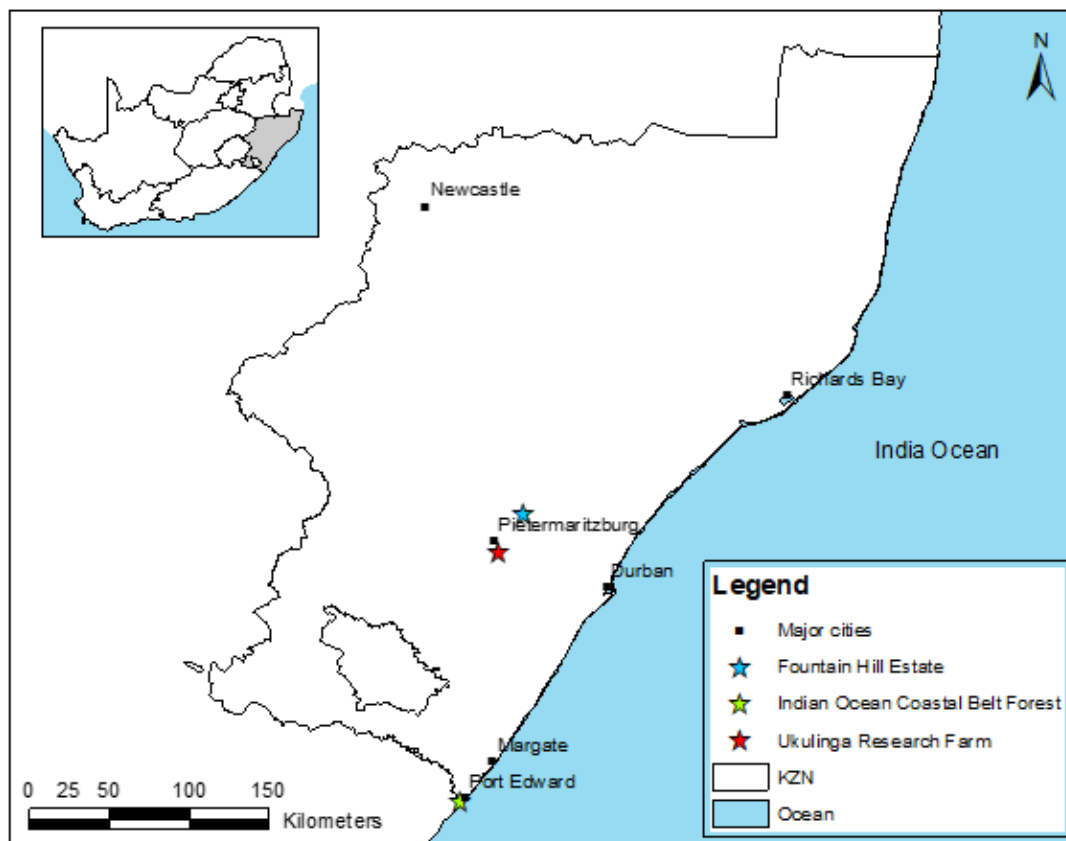


Fig. 1.2. Location of study sites in KwaZulu-Natal Province, South Africa in the present study.

1.12 Problem statement

Biological invasions are recognised as a major problem globally threatening biodiversity (Davies et al., 2016). In South Africa, alien invasive plant species are the most diverse and damaging invasive and fleshy-fruited invasive species are a major problem (Thabethe et al., 2015). The invasiveness potential of fleshy-fruited invasive plant species is increased as these plants integrate into seed dispersal networks and mutual relationships with native dispersers (Jordaan and Downs, 2012; Thabethe et al., 2015). Dispersers of fleshy-fruited plants with relatively small fruits that have been recognised include avian species (Traveset and Willson, 1997; Wotton and Kelly, 2012), primates (Chapman and Russo, 2007; McConkey, 2018). The successful spread of *L. camara* has been associated with mutual relationships with native seed dispersers. In South Africa, not a lot of work had been done to determine the assemblage of

avian species feeding on *L. camara* (Taylor et al., 2018). Most studies on avian mediated seed dispersal of the plant have been focused on the influence of bird species on the germination success of the plant. Therefore, the present study will fill an important knowledge gap that is needed for effective management of *L. camara* and biodiversity conservation.

Habitat fragmentation poses a threat to biodiversity and in forest systems it creates disturbance zones that are associated with increased invasion (Balaguru et al. 2016). Alien invasive plants in South Africa are managed when they are widespread (van Wilgen 2018) and therefore predictive approaches should be developed to understand invasion dynamics. Seed dispersal is influenced by the functional traits of both the plant and animal (Tiribelli et al., 2017). Thus, a functional trait approach can be used to understand seed dispersal of fleshy-fruited invasive plant species. To my knowledge in Southern Africa there has not been a study that has adopted a functional trait approach to predict avian seed dispersers of fleshy-fruited invasive species. Therefore, the present study will contribute knowledge that has management implications relating to forest management. Impacts associated with alien invasive species vary in magnitude and mechanism as a result species are listed into different categories for management prioritisation (Kumschick et al., 2017). In South Africa, the listing of species into different categories was based on expert opinion. Expert-based opinion listing of species is often subjective and not comparable across different habitats and taxa groups. Consequently, comprehensive quantitative assessment of alien invasive plant species impacts is generally lacking (Moshobane et al., 2019). Therefore, knowledge of top priority species with major threats are being prioritised for management is limited. Considering that alien invasive plant species management is limited by insufficient funds, it is important to assess the impacts of alien invasive plants to guide allocation of limited resources.

1.13 Aims and objectives

The main aim of the present study was to assess the importance of native bird species in the seed dispersal of fleshy-fruited invasive plant species and the ecological and socio-economic impacts of fleshy-fruited invasive plant species. The objectives of the study were to determine:

1. Avian dispersers of fleshy-fruited invasive using a functional trait approach
2. The assemblage of avian species that are dispersing *L. camara* seeds and the potential dispersal distances that ingested seeds are dispersed over.
3. The ecological and socio-economic impacts associated with fleshy-fruited invasive plant species.

1.14 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 four chapters (Chapter 2, 3 and 4) are experimental data chapters with each one covering a specific objective. Each chapter is formatted according to the journal it is intended to be (or has been) submitted to. 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. Chapter 2 investigated avian seed dispersers of fleshy-fruited invasive plant species. Chapter 3 investigated the avian species assemblage dispersing the seeds of *L. camara*. Chapter 4 investigated the ecological and socio-economic impacts posed by fleshy-fruited invasive plant species. The final chapter (Chapter 5) discusses the main findings of the study and their management implications.

1.15 References

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CHAPTER 2

Predicting avian dispersers of fleshy-fruited invasive plant species from bird and plant functional traits

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Running header: Predicting seed dispersal from functional traits

2.1 Abstract

Habitat fragmentation has a multitude of negative effects on biodiversity, including the facilitation of alien plant invasion. Of concern in South Africa is the spread of fleshy-fruited invasive plant species, which in many places are replacing indigenous vegetation in frequently disturbed and fragmented habitats. The availability of dispersers is the most important factor for the successful invasion of fleshy fruited invasive plant species. Dispersers differ in their dispersal capacity and the success of frugivore dispersed plants depends both on animal and plant traits. Here, we used the functional traits of fleshy-fruited invasive plants (i.e. fruit size, seed size, number of seeds, crop size, plant habitat, plant height, fruiting period and a derived invasiveness score) to test for specific associations with avian functional traits (i.e. gape size, bill length, body mass, degree of frugivory, foraging strategy, abundance and habitat specificity) in Indian Ocean Coastal Belt Forests, KwaZulu-Natal Province, South Africa. We predicted that fleshy-fruited invasive plant species that were more likely to persist in disturbed Indian Ocean Coastal Belt Forests were small-seeded, open habit species with longer fruiting period lengths. Through multivariate analyses, we found native avian forest species that are potentially effective seed dispersers were forest habitat generalist and relatively abundant species. Overall, our study showed that using easily measured metrics is important for understanding forest invasion dynamics and can give insights to management strategies that can be developed to minimise further infestations.

Keywords: forest invasions; fragmentation; functional traits; multivariate analysis; seed dispersal

2.2 Introduction

Habitat fragmentation is presently one of the most threatening impacts on forest ecosystems worldwide, impacting biodiversity and reducing seed dispersal and recruitment of organisms (Levey et al. 2005; Niu et al. 2018). This leads to altered ecological processes (McConkey and O’Farrill 2016; Liebhold et al. 2017), changes in species composition, and reduced functional diversity (Bovo et al. 2018). Human activities are isolating and decreasing the sizes and quality of forest habitats (Gosper et al. 2005; Vardien et al. 2012; Habel et al. 2016; Mavimbela et al. 2018), creating disturbance zones that are associated with increased invasion rates (Brothers and Spingarn 1992; Balaguru et al. 2016). Biological invasions disturb ecosystem functioning and are associated with negative socio-economic impacts (Liebhold et al. 1995; SANBI 2017), and as such are major threat to biodiversity (Wilson et al. 2013; Blackburn et al. 2019) and human livelihoods (Wilson et al. 2013; Liebhold et al. 2017). Like other parts of the world (Niu et al. 2018), forests in South Africa are under threat of alien invasive plants (Mucina et al. 2006; Henderson 2007; SANBI 2017; Mavimbela et al. 2018). Increased human dominance surrounding forest patches, economic pressures, high-intensity agriculture, growing human needs (Mucina 2006) and urbanisation (Cho et al. 2015) are among the factors that relate to disturbance of the South African forests.

Seed dispersal (i.e. the movement of seeds from parent plant to novel establishment sites) is critical for the maintenance of plant communities (Jordano et al. 2007; Wilson and Downs 2012a, b; Carrion-Tacuri et al. 2012; Lindgren et al. 2018), colonisation of new sites (Russo et al. 2006; Corlett 2017), alien invasions (Buckley et al. 2006; Schupp et al. 2010) and has important management implications (Spiegel and Nathan 2007; Gosper and Vivian-Smith, 2009). Seed dispersal is particularly important for tropical and sub-tropical ecosystems as 90% of fleshy fruiting plants rely on frugivores for dispersal (Howe and Smallwood 1982; Wilson and Downs 2012a, b). Frugivore-mediated dispersal deposits seed away from parent and

siblings reducing competition and predation rates leading to colonisation of new sites given that they are suitable for establishment (Gosper et al. 2005; Lindgren et al. 2018). Alien invasive plant species integrate into local dispersal networks by forming mutualistic relationships with local dispersers for dispersal services (Voigt et al. 2011) resulting in increased plant invasions risk (Gosper et al. 2005; Neilan et al. 2006; Jordaan et al. 2011). Successful alien invasive plant species have reproductive strategies (e.g. large crop sizes, small seed sizes) that increase the chances of forming mutual relationships with frugivores that function as seed vectors (Cordeiro et al. 2004; Jordaan et al. 2011). Many invasive plant species are predominantly dispersed by native bird species (Gosper et al. 2005; Gooden et al. 2009; Richardson and Rejmanek 2011; Carrion-Tacuri et al. 2012; Jordaan et al. 2011; Mokotjomela et al. 2015; Dlamini et al. 2018) and therefore influence conservation concerns (Carrion-Tacuri et al. 2012). Birds benefit by gaining a new food source and invasive plant species benefit mainly by having their seeds dispersed (Gosper et al. 2005; Jordaan et al. 2011).

Species' responses to disturbance and their effects on ecological processes is determined by their functional traits (Gosper et al. 2005; da Silveira Ponte et al. 2015; Carmona et al. 2016); hence, functional traits provide an alternative approach to understand ecological processes. Functional traits are defined as those that influence ecosystem functioning (De Deyn et al. 2008; Drenovsky et al. 2012; Bender et al. 2018). Dispersal services offered to a plant are dependent on both animal and plant traits (Jordano 2000; Gosper et al. 2005; Buckley et al. 2006, Gosper and Vivian-Smith 2009). The traits of a disperser influence the quality and quantity of dispersal received by the plant that includes which, when and how many seeds are dispersed and their germination success (Schupp 1993; Buckley et al. 2006; Jordano et al. 2007). Frugivore traits influence the capacity of the frugivores to disperse seeds, resulting seed shadow (Jordano 2000; Gosper et al. 2005; Jordano et al. 2007; Martin-Albaracin et al. 2018) and the ability of birds to find and consume fruit (Gosper and Vivian Smith 2009; Wilson and

Downs, 2012 a, b). These include frugivore movement (Buckley et al. 2006; McConkey et al. 2012; Martin-Albaracin et al. 2018), dietary composition (Jordano 2000; Gosper et al. 2005; Novak et al. 2018), frugivore body size (Kitamura et al. 2002; Jordano et al. 2007; Bovo et al. 2018), feeding technique, and gape width (Jordano 2000; Symes and Downs 2001; Wilson and Downs 2012a, b; Bovo et al. 2018). Plant traits that can influence the probability of dispersal include fruit morphology, seed size, crop size and fruit density (Gosper et al. 2005; Buckley et al. 2006; Gosper and Vivian Smith 2009; Bender et al. 2018, number of seeds per fruit, fruit size (Jordano 2000; Buckley et al. 2006; Jordaan et al. 2011; Jordaan and Downs, 2012a, b), fruit colour (Richardson et al. 2000; Buckley et al. 2006; Wilson and Downs 2012a, b), and plant height (Blendinger and Villegas 2011; Bender et al. 2018). Fruit size limits the plant-frugivore interactions (Symes and Downs 2001; Kitamura et al. 2002; Gosper and Vivian Smith 2009; Wilson and Downs 2012a, b), as it determines if the fruit can be swallowed or pecked (Levey 1987; Jordano 2000; Symes and Down, 2001). Functional traits of species often covary and therefore should not be considered in isolation, but rather in pairs or groups (da Silveria Ponte et al. 2015). Ecological processes that are mediated by species' interactions are most suitable for using a functional trait approach as it allows for comparing species traits of interacting species (Dehling et al. 2016).

Invasion by fleshy-fruited invasive plant species is a major problem in South Africa (Henderson 2001; Richardson and van Wilgen 2004; Thabethe et al. 2015). These species are predominantly bird-dispersed in forest systems (Henderson 2007; Mora and Smith-Ramírez 2016). Our present study focused on fleshy-fruited invasive shrubs and trees with distributions that overlapped with the Indian Ocean Coastal Belt Forests in South Africa. Understanding forest dynamics includes the need to disentangle plant-animal mutualisms and frugivory (Mucina et al. 2006). Understanding how alien invasive species invade new habitats is critical (Cordeiro et al. 2004; SANBI 2017) particularly in South Africa as a high proportion of

biodiversity is supported by forests relative to its small land cover (Henderson 2007; Wilson and Downs 2012 a, b; Poulsen and Hoffman 2015; Mensah et al. 2016). Studies of frugivore-mediated dispersal are important for understanding the spread of invasive plant species (Gosper et al. 2005), how frugivore populations are affected by these invasive species, and improving management of invasive plants (Gosper et al. 2005; Buckley et al. 2006, Neilan et al. 2006). In South Africa, invasive species are usually managed once they are widely spread (Wilson et al. 2013). Therefore, developing an approach that is based on functional traits is valuable as it allows for the prediction of possible interactions and is key for generalisation and management of invasive plants at early invasion stages and predicting future invasions. Trait-based approaches to seed dispersal studies are lacking and highlight the importance of filling these gaps (Garcia et al. 2016). A predictive approach is important for conservation planning, prioritising forest invasion management (Balaguru et al. 2016; SANBI 2017) and reducing uncertainty in management (da Silveria Ponte et al. 2015).

Most studies on seed dispersal in forest systems have mainly focused on forest regeneration of indigenous species and not on the fleshy-fruited invasive plant species. To date, no study in Africa has adopted a functional trait approach to predict seed dispersers of alien fleshy-fruited. Here, we aimed to predict native avian dispersers of fleshy-fruited invasive plant species into forest ecosystems based on the functional traits of both plant and bird species. Specifically, we asked (1) which fleshy-fruited plant species will be dispersed by avian species in fragmented Indian Ocean Coastal Belt Forests, (2) which avian species may contribute to the dispersal of fleshy-fruited invasive plant species, and (3) can we predict spread of fleshy-fruited alien invasive plant species based on the key functional traits identified and the distribution of avian dispersers. Human activities are causing fragmentation and degradation that alters the native species abundance and composition of species assemblages (Gosper et al. 2005; Fontúrbel et al. 2017) and forest specialists decline with increased forest disturbance.

For this study, we predicted that fleshy-fruited alien invasive plants will be dispersed by generalist bird species that persist in fragmented forest patches.

2.3 Methods

2.3.1 Plant functional traits

We selected 11 fleshy-fruited invasive plant species (Table 2.1) that are listed under the South African National Environmental Management: Biodiversity Act (NEM: BA), that are bird-dispersed, and are invading the Indian Ocean Coastal Belt Forests. NEM: BA categories were provided by the government of South Africa after recognising the threats that are posed by invasive plants under the Conservation of Agricultural Resources Act (CARA; Act No. 43 of 1983) (Cronin et al. 2017). Category 1 species are prohibited, and their characteristics pose a threat to the environment, humans and animals (Henderson 1995; Henderson 2001; Bromilow 2010). Category 2 species may only be grown under demarcated areas and must be controlled (Henderson 1995; Henderson 2001; Bromilow 2010). Category 3 plant species can be grown but should not be planted or traded, and existing plants must be prevented from spreading (Henderson 1995; Henderson 2001; Bromilow 2010). For all plant species, we compiled eight functional traits (Table 2.2; fruit size, seed size, number of seeds, habitat type, plant height, invasiveness, fruiting period length and crop size) that influence the potential of plants to be dispersed (Gosper and Vivian-Smith 2009; 2010; Garcia et al. 2016; Corlett 2017). The data were compiled from existing literature, except for crop sizes that were unavailable in the literature for some species. To quantify seed fruit crop size of the plants we calculated the number of seeds on three 1 m branches in a tree, calculated the number of branches, and measured the height and diameter at breast height (DBH) of the tree. For each species these measurements were done for a minimum of five individuals. Invasiveness score categories were created using the NEM: BA categories, risk assessment scores and used the Global

Biodiversity Information Facility (GBIF) for the species occurrence records in South Africa. The scores ranged from least invasive (= 1) invasive to highly invasive (= 5).

2.3.2 Bird species assemblage and functional traits

To characterise potential avian dispersers for this study, we used point-count surveys of the Indian Ocean Coastal Belt Forests (for detailed avian species survey see Ehlers Smith et al. 2018) and filtered by frugivorous species. The frugivore community comprised of 58 species (Supplementary information Table S2.1), and for each frugivorous bird species we compiled their functional trait data that generally influences avian seed dispersal, including bird body mass, bill length, gape width, habitat specificity (forest specialist or generalist), frugivory (obligate or partial frugivorous), gregariousness (solitary or gregarious), foraging position (ground specialist; canopy special; various positions) and abundance (rare = 1; 2 = uncommon; 3 = fairly or locally common; 4 = common; 5 = very common or abundant) from existing literature (Hockey et al. 2005; Supplementary information Table S2.1). Gape width was measured using the bird species collection at the Durban Natural Science Museum, Durban, South Africa. For each bird species, we measured the gape size using digital calipers of 20 individuals (10 per sex); if there were fewer than 10 individuals we measured as many individuals as were available. All the functional traits data were then compiled into a species trait matrix.

Table 2.1. Fleshy-fruited invasive species used in this study, categorised according to the Conservation of Agricultural Resources Act (Act 43 of 1983) invading Indian Ocean Coastal Belt Forests of KwaZulu-Natal, South Africa.

Invasive plant species	Common name	Family name	Invasion category	Species area of origin
<i>Ailanthus altissima</i>	Tree of heaven	Simaroubaceae	1b	China
<i>Ardisia crenata</i>	Coral bush	Primulaceae	1b	Asia
<i>Cinnamomum camphora</i>	Camphor tree	Lauraceae	1b	East Asia
<i>Duranta erecta</i>	Forget-me-not-tree	Verbenaceae	3	America
<i>Lantana camara</i>	Lantana	Verbenaceae	1b	Central and South America
<i>Melia azedarach</i>	Syringa	Meliaceae	1b	Asia, Australia
<i>Morus alba</i>	White mulberry	Moraceae	2	Asia
<i>Psidium guajava</i>	Guava	Myrtaceae	2	America
<i>Ricinus communis</i>	Castor-oil plant	Euphorbiaceae	1b	Africa
<i>Schinus terebinthifolius</i>	Brazilian pepper tree	Anacardiaceae	1b	Brazil
<i>Solanum mauritianum</i>	Bugweed	Solanaceae	1b	South America

Table 2.2. Functional traits recorded of fleshy-fruited plant species invading Indian Ocean Coastal Belt Forests in the present study.

Scientific name	Mean fruit size (mm)	Mean seed size (mm)	Mean number of seeds	Fruiting period length (month)	Mean fruit crop size	Mean plant height (m)	Habitat	Invasi score
<i>Ardisia crenata</i>	8.4	5.4	1.0	3	1200.0	1.5	Forest	2.1
<i>Ailanthus altissima</i>	5.7	4.0	1.0	4	325000.0	7.5	Forest	4.7
<i>Cinnamomum camphor</i>	8.0	6.5	1.0	3	100000.0	25	Forest	4.6
<i>Duranta erecta</i>	7.0	3.5	4.0	4	25325.0	3.5	Forest	1.7
<i>Lantana camara</i>	4.0	3.0	1.5	4	856.0	2.0	Open	5.0
<i>Melia azedarach</i>	11.9	9.0	5.0	3	14756.0	12.0	Forest	3.0
<i>Morus alba</i>	9.1	1.8	29.0	4	86000.0	7.50	Open	3.0
<i>Psidium guajava</i>	45.2	2.4	276.0	3	1326.0	3.0	Open	3.1
<i>Ricinus communis</i>	20.0	7.0	3.0	3	84.0	3.0	Open	3.8
<i>Schinus terebinthifolius</i>	1.0	2.9	1.0	4	10000.0	4.0	Open	4.1
<i>Solanum mauritianum</i>	13.7	1.5	182.0	4	150000.0	6.0	Open	4.1

2.3.3 Data analyses

To identify relationships between functional traits of fleshy-fruited invasive plant species and avian seed dispersers in Indian Ocean Coastal Belt Forests, a Principal Component Analysis (PCA) was applied separately. Principal component analyses were used to visualise the distribution of the eight invasive plant species and the 58 avian species in relation to their functional traits. Data visualisation was performed using ‘ggbiplot’ in R Statistical Software (R Core Team 2018).

2.4 Results

The PCA of the seven invasive plant functional traits explained 62.3% of the variation (Fig. 2.1). The first PCA axes (PC1) were positively correlated with the number of seeds and fruit size, which increased along the axes and negatively correlated with habitat type and plant height (Fig. 2.1; Table 2.2). The second axes (PC2) were positively correlated with fruit size and seed size, which increased along the axes and negatively correlated with fruiting period length, crop size and invasiveness (Fig. 2.1, Table 2.3). Guava *Psidium guava* was separate from the other plant species in the ordination which was explained by its relatively large fruit size and high number of seeds (Table 2.2). The species in the lower right quadrant of the ordination consisted of lantana *Lantana camara*, white mulberry *Morus alba* and Brazilian pepper tree *Schinus terebinthifolius*. These plant species are generally characterised by small fruit and seed size, high invasiveness scores and long fruiting periods (Table 2.2). Plant species in the upper right quadrant of the ordination included syringa *Melia azedarach*, camphor tree *Cinnamomum camphora*, castor-oil plant *Ricinus communis* and coral bush *Ardisia crenata*, which are characterised by relatively large seed sizes (> 5 mm) (Table 2.2).

The first two components of the eight functional bird traits influencing the dispersal ability of 58 avian species in Indian Ocean Coastal Belt Forests explained 56.1 % of the variability. The first axis of the PCA (PC1) explained 36.3 % of the variation and was strongly positively correlated to the bird body mass, gape width and bill length (Figure 2.2, Table 2.3). Avian species clustered in the upper quadrant of the ordination consisted of the speckled mousebird *Colius striatus*, dark-capped bulbul *Pycnonotus tricolor*, red-winged starling *Onychognathus morio* and thick-billed weaver *Amblyospiza albifrons*. These avian species are medium-sized, common or abundant, forest generalised, obligate frugivores that flock (> 20) or form small groups (> 4) in Indian Ocean Coastal Belt Forests (Supplementary information Table S2.1). The second axis explained 19.3 % of the variation and was correlated strongly with abundance, gregarious and obligate frugivores and was negatively correlated with forest specialists (Figure 2.2, Table 2.3). The species in the lower quadrant consisted of the tambourine dove *Turtur tympanistra*, white-starred robin *Pogonocichla stellata* and brown scrub-robin *Cercotrichas signata* which are forest specialists, uncommon or fairly common species, solitary or in pairs and partial frugivores in Indian Ocean Coastal Belt Forests (Supplementary information Table S2.1). From the eight avian functional traits, there were sets of correlated traits. The first set included bird gape width, bill length and body mass. The second set included gregariousness and obligate frugivores. From the plant species traits, the first set of correlated traits included plant fruiting crop size, fruiting period length and invasiveness. The second set included habitat and plant height.

Table 2.3. Eigenvector scores of fleshy-fruited invasive plants and Indian Ocean Coastal Belt Forests bird species in functional traits based on the first two axes of the Principle Component Analysis in the present study. Numbers highlighted in bold represent positive correlation.

Plant species functional traits	PC1(33.7%)	PC2 (28.6 %)
Number of seeds	0.47	0.20
Seed size	-0.47	0.34
Fruit size	0.36	0.44
Habitat	-0.49	0.08
Fruiting period length	0.17	-0.59
Crop size	-0.11	-0.41
Plant height	-0.38	0.10
Invasiveness	-0.02	-0.34
Bird species functional traits	PC1(41.5 %)	PC2 (16.3 %)
Body mass	0.51	-0.06
Gape width	0.54	-0.13
Bill length	0.52	-0.17
Forest specialist	0.08	-0.38
Obligate frugivore	0.28	0.39
Gregarious	0.31	0.42
Foraging position	-0.05	0.07
Abundance	-0.02	0.67

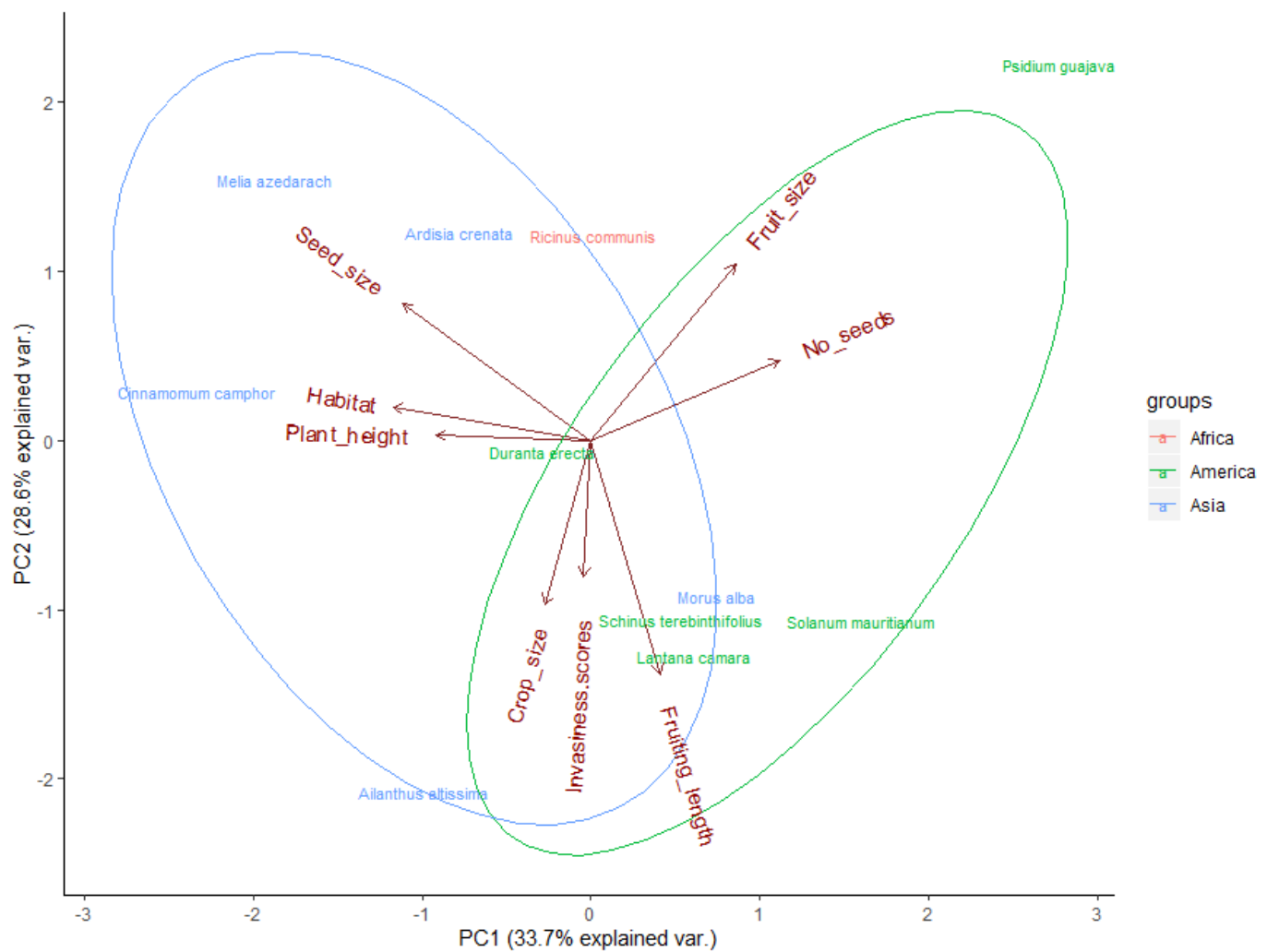


Fig 2.1. Principle Component Analysis axes based on the invasiveness scores and seven functional traits influencing the seed dispersal of 11 fleshy-fruited invasive plant species invading Indian Ocean Coastal Belt Forests of KwaZulu-Natal, South Africa in the present study. The axes explained 62.3% of variance using PC1 and PC2. Ellipses indicate native ranges of the invasive plant species.

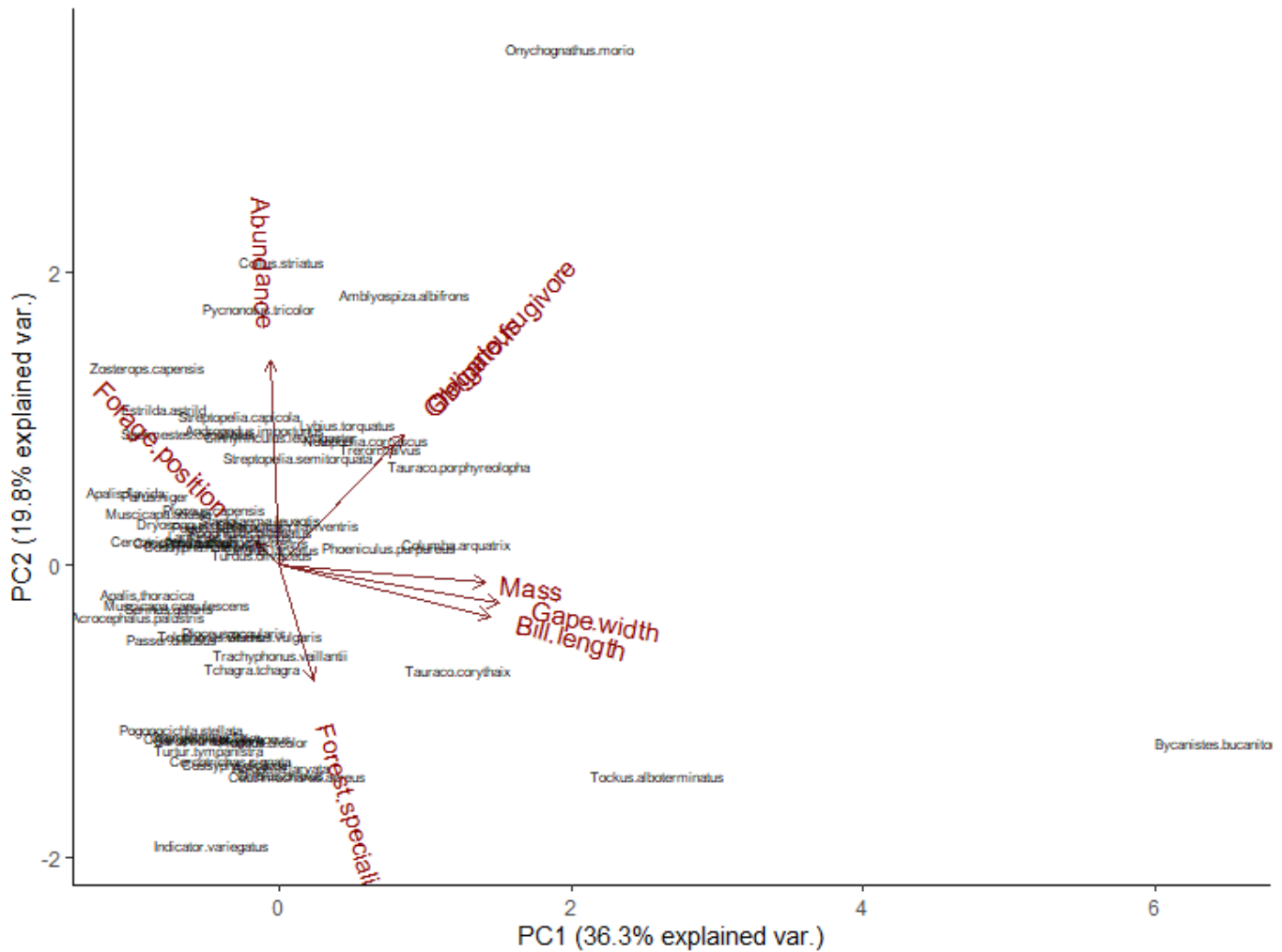


Fig 2.2 Principal Component Analyses of eight functional traits that influence the seed dispersal ability of 58 avian species observed in the Indian Ocean Coastal Belt Forests of KwaZulu-Natal, South Africa in the present study. The first two components explained 56.1 % of variance.

2.5 Discussion

Improving understanding and responding to biological invasions in terms of policy and effective management requires predictive approaches (Drenovsky et al. 2012). Our study aimed to understand the invasion dynamics in Indian Ocean Coastal Belt Forests of KwaZulu-Natal Province, South Africa, using a functional trait-based approach. Among the fleshy-fruited

invasive plant species, the variation of the traits described plant species fruit morphology (fruit size, seed size and number of seeds), phenology (fruiting period length), fruit crop size and plant height. Our results showed that fleshy-fruited invasive plant species differed in their morphological traits that influence their seed dispersal ability. These results were consistent with other studies that have shown that fleshy-fruited species vary in morphological and phenology traits that are important functional traits influencing the interaction of fleshy-fruited plants with their avian dispersers (Symers and Downs 2001; Chimera and Drake 2010; Gosper and Vivian-Smith 2010; Wotton and Mc Alpine, 2015; Muñoz et al. 2017; Ramos-Robles et al. 2018). Functional trait variations in plant species are driven by trade-offs of co-varying traits (e.g. seed size and fruit size) or other factors and this can be beneficial to plants if the preference of dispersers varies (Muñoz et al. 2017; Zwolak 2018). Fleshy-fruited invasive species characterised by small seeds usually have more frugivorous visits compared with multi-seeded large fruits (Aslan 2011; Muñoz. 2017; Dlamini et al. 2018). Also, invasive plants species generally germinate faster than large seeds especially in disturbed environments (Jordaan and Downs 2012b). Avian frugivores prefer small sized fruits so that they reduce handling time and maximise their daily energy (Symes and Downs 2001). Plant species like lantana, Brazilian pepper tree, and white mulberry are generally open habitat species characterised by smaller seed size and fruit size (< 5 mm) and bird species in the Indian Ocean Coastal Belt Forests may be benefiting from these plants species and facilitating their seed dispersal. Frugivorous avian species have been reported to prefer foraging in fleshy-fruited species that are along the margins of forest gaps (Mokotjomela et al. 2013). Therefore, the open habitat species have the advantage of having to have more frequent visitations by bird species. Another important trait of these species is long fruiting period lengths and relatively large crop sizes that may guarantee food availability to avian species. Fleshy-fruited invasive species with longer fruiting periods and large fruit crop sizes tend to be more successful as they provide fruits when native species

are out of fruit (Aslan 2011; Martin-Albaracin et al. 2018). Also, fruiting plant species with large crop sizes are more likely to attract highly frugivorous species so that they can maintain their daily energy requirements (Bender et al., 2018). Therefore, these species have higher invasiveness potential as they can interact and be consumed by the entire communities as opposed to large-seeded species (syringa, castor-oil plant, camphor tree) that can only be consumed by a few large bird species with a large gape width, which limits their dispersal ability.

Among the avian species, there were variations in functional traits that influenced the ability of bird species to be effective seed dispersers. The first variation related to the bird species morphology (mass, gape width, bill length) and the second variation related to level of frugivory, gregariousness, abundance, and forest-dependence. Variation in morphological traits of bird species results from environmental effects during developmental stages (Telleria et al. 2013) and anthropogenic related disturbances (de Assis Bomfin et al. 2018; Bovo et al. 2018). Variations in functional traits for frugivorous bird species relate more to body size (Bregman et al. 2016), abundance and gape width (Gonzalez-Castro et al. 2015) and level of frugivory (Carlo and Morales 2016; Sebastian-Gonzalez 2017). Therefore, disturbance may account for the variation in body mass of the bird species in this study. The most important and effective dispersers of fleshy-fruited invasive plant species were potentially the abundant, obligate frugivorous and forest generalist species such as speckled mousebird, dark-capped bulbul, red-winged starling and thick-billed weaver. Dark-capped bulbuls and speckled mousebird meet their daily energetic demands from the fruits of invasive plant species particularly Lantana (Jordaan and Downs 2012b). Obligate frugivorous species are effective seed dispersers as they are associated with increased visitation frequencies and more interactions with fruiting species (Schleuning et al. 2011; de Assis Bomfin et al. 2018). However, increased visitation is not always associated with effective seed dispersal (Cordeiro,

2009). Their large gape width also allows for the consumption of a range of seed sizes. Size overlap between gape width and fruit size has been shown to be the most important in determining plant-frugivore interactions (Symes and Downs, 2001; Gonzalez-Castro et al. 2015). Consistent with our hypotheses, these patterns suggest that the more abundant forest generalists are potentially more effective in the seed dispersal of fleshy-fruited invasive species. Most forest specialists were partial frugivores, less abundant and are unlikely to be effective seed dispersers of fleshy-fruited invasive plant species.

In the present study, invasive fleshy-fruited species that are more likely to be a major problem in Indian Ocean Coastal Belt Forests of KwaZulu-Natal are open habitat shrub or trees that were more likely not dispersal limited and this included lantana, Brazilian pepper tree, white mulberry and bugweed. Similarly, Indian Ocean Coastal Belt Forests in Durban are invaded by shade-intolerant invasive trees or shrubs that thrive in canopy gaps (Mavimbela et al. 2018). The shade-tolerant species, namely castor oil plant, syringa, camphor and coral bush are less likely to be a major problem in coastal forests as they are dispersal limited because of their relatively large seed size ($> 5\text{mm}$) and the absence of relatively large bird species.. In forest systems mammals provide complementary seed dispersal services to fleshy-fruited plant species (Wotton and McAlpine, 2015; Corlett 2017). Therefore, the large seeded plant species may be benefiting from other dispersers like ungulates and primates within the Indian Ocean Coastal Belt Forests. Also, most effective bird species that can potentially disperse the fleshy-fruited invasive plant species were the abundant forest generalist species that persist in fragmented forests. Therefore, exotic plant invasions are more likely to be along forest margins or within forest gaps. This highlights the importance of conservation strategies that aim to reduce habitat loss or forest destruction to create recruitment barriers of invasive species that are not dispersal limited and reduce further infestations. The main limitation of a trait-based approach is that it requires strong understanding of the system (Brym et al. 2011). Therefore,

the predictions of this study are applicable to the Indian Ocean Coastal Belt Forests of KwaZulu-Natal and this generalisation should be applied cautiously in other systems.

2.5.1 Conclusions

Determining invasion dynamics in forests using a functional trait approach provides insights on the potential avian seed dispersers of fleshy-fruited invasive species and the potential distribution of future infestations. In this study, we have shown that both fleshy-fruited invasive plant and bird species vary in their traits that influence seed dispersal interactions. The findings of this study have implications for conservation as screening of functional traits or measuring easily measured metrics can give insights on the invasive dynamics in forest systems. Using a functional trait approach showed the fleshy-fruited invasive plant species that are more likely to persist in fragmented coastal forests of KwaZulu-Natal are lantana, white mulberry, Brazilian pepper tree and bugweed. Opened habitats within forests should be monitored for management as there are more susceptible to invasions by highly invasive plant species. Considering the functional differences between fleshy-fruited invasive plant species we suggest that forest management prioritise management of small-seeded invasive plant species with large fruit crop sizes and longer fruiting period lengths as they have a more invasiveness potential. These traits can also be used to determine species with a high invasiveness potential during screening protocols (Jordaan and Downs, 2012b). The findings of this study could be used as a baseline for creating a more complex functional-based model including other guilds for predicting forest invasions.

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2.8 Supplementary information

2 **Supplementary information Table S2.1.** Functional traits of the avian frugivore community of the Indian Coastal Belt Forests, South Africa in the present study.

Scientific names	Common names	Mean body mass (g)	Mean gape width (mm)	Mean bill length (mm)	Forest specialist	Obligate frugivore
<i>Acrocephalus palustris</i>	Marsh warbler	11.0	5.5	16.6	No	No
<i>Amblyospiza albifrons</i>	Thick-billed weaver	56.0	12.9	21.1	No	Yes
<i>Andropadus importunus</i>	Sombre greenbul	31.0	8.6	19.4	No	Yes
<i>Apalis flavida</i>	Yellow-breasted apalis	8.0	4.8	13.6	No	No
<i>Apalis thoracica</i>	Bar-throated apalis	10.5	4.4	14.7	Yes	No
<i>Aplopelia larvata</i>	Lemon dove	150.0	8.5	21.3	Yes	No
<i>Bycanistes bucinator</i>	Trumpeter hornbill	644.0	34.7	124.0	Yes	Yes
<i>Campephaga flava</i>	Black cuckooshrike	32.0	10.5	15.0	No	No
<i>Cercotrichas leucophrys</i>	White-browed scrub robin	17.9	7.7	17.9	No	No
<i>Cercotrichas signata</i>	Brown scrub robin	38.0	8.2	22.4	No	No
<i>Ceuthmochares aereus</i>	Green malkoha	70.0	13.8	26.5	No	No
<i>Chlorocichla flaviventris</i>	Yellow-bellied greenbul	40.0	8.5	21.0	No	Yes
<i>Chlorophoneus olivaceus</i>	Olive bushshrike	33.0	8.5	21.7	Yes	No
<i>Cinnyricinclus leucogaster</i>	Violet-backed starling	45.0	10.7	18.2	No	Yes
<i>Colius striatus</i>	Speckled mousebird	55.0	9.1	12.9	No	Yes
<i>Columba arquatrix</i>	African olive pigeon	407.0	9.4	24.1	No	Yes
<i>Cossypha caffra</i>	Cape robin-chat	28.0	7.9	15.7	No	No
<i>Cossypha dichroa</i>	Chorister robin-chat	46.0	8.8	20.5	Yes	No
<i>Cossypha natalensis</i>	Red-capped robin-chat	32.0	9.2	16.8	No	No
<i>Dryoscopus cubla</i>	Black-backed puffback	26.0	8.8	19.0	No	No
<i>Estrilda astrild</i>	Common waxbill	8.0	4.9	10.9	No	No

<i>Indicator variegatus</i>	Scaly-throated honeyguide	48.0	8.9	12.2	Yes	No
<i>Laniarius ferrugineus</i>	Southern boubou	60.0	9.8	24.0	No	No
<i>Lybius torquatus</i>	Black-collared barbet	54.0	13.6	22.7	No	Yes
<i>Muscicapa adusta</i>	African dusky flycatcher	11.0	7.7	14.9	No	No
<i>Muscicapa caerulescens</i>	Ashy flycatcher	16.5	8.9	11.5	No	No
<i>Notopholia corruscus</i>	Black-bellied starling	50.0	10.3	21.3	Yes	Yes
<i>Onychognathus morio</i>	Red-winged starling	140.0	13.6	32.7	No	Yes
<i>Oriolus larvatus</i>	Black-headed oriole	65.0	11.6	30.5	No	No
<i>Oriolus oriolus</i>	Eurasian golden oriole	64.0	12.4	27.5	No	No
<i>Parus niger</i>	Southern black tit	21.0	7.3	11.0	No	No
<i>Passer diffusus</i>	Southern grey-headed sparrow	24.0	7.1	13.8	No	No
<i>Phoeniculus purpureus</i>	Green wood-hoopoe	76.0	13.9	54.2	No	No
<i>Phyllastrephus terrestris</i>	Terrestrial brownbul	31.5	10.3	22.0	No	No
<i>Ploceus bicolor</i>	Dark-backed weaver	35.0	11.8	22.4	Yes	No
<i>Ploceus capensis</i>	Cape weaver	46 .0	8.2	23.5	No	No
<i>Ploceus occularis</i>	Spectacled weaver	30.0	11.2	21.6	No	No
<i>Pogoniulus bilineatus</i>	Yellow-rumped tinkerbird	15.0	9.0	12.9	Yes	Yes
<i>Pogoniulus pusillus</i>	Red-fronted tinkerbird	17.0	8.2	12.6	No	Yes
<i>Pogonocichla stellata</i>	White-starred robin	21.0	7.3	16.0	Yes	No
<i>Pycnonotus tricolor</i>	Dark-capped bulbul	37.3	9.3	19.2	No	Yes
<i>Sarothrura elegans</i>	Buff-spotted flufftail	45.0	7.0	16.6	Yes	No
<i>Serinus gularis</i>	Streaky-headed seedeater	20.0	7.4	11.7	No	No
<i>Spermestes cucullatus</i>	Bronze mannikin	10.0	6.0	9.8	No	No
<i>Stactolaema leucotis</i>	White-eared barbet	54.0	7.3	19.2	No	Yes
<i>Streptopelia capicola</i>	Cape turtle-dove	150.0	7.2	15.7	No	No
<i>Streptopelia semitorquata</i>	Red-eyed dove	235.0	8.7	21.8	No	No
<i>Sturnus vulgaris</i>	European starling	80.0	8.9	29.2	No	No

<i>Tauraco corythaix</i>	Knysna turaco	310.0	12.6	23.5	Yes	Yes
<i>Tauraco porphyreolopha</i>	Purple-crested turaco	300.0	14.5	24.9	No	Yes
<i>Tchagra tchagra</i>	Southern tchagra	47.0	9.4	30.6	No	No
<i>Telophorus viridis</i>	Gorgeous bushshrike	37.0	9.5	21.2	No	No
<i>Tockus alboterminatus</i>	Crowned hornbill	225.0	23.9	88.5	No	No
<i>Trachyphonus vaillantii</i>	Crested barbet	70.0	13.6	24.2	No	No
<i>Treron calvus</i>	African green pigeon	235.0	11.1	21.1	No	Yes
<i>Turdus olivaceus</i>	Olive thrush	66.0	11.4	22.2	No	No
<i>Turtur tympanistra</i>	Tambourine dove	71.0	6.7	15.6	Yes	No
<i>Zosterops capensis</i>	Cape white-eye	13.5	5.6	13.6	No	No

CHAPTER 3

Potential dispersal of invasive *Lantana camara* by native bird species in KwaZulu-Natal, South Africa

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Running header: Potential dispersal of invasive *L. camara* by native bird species

3.1 Abstract

Alien invasive plant species are a major problem globally, threatening ecosystem functioning and biodiversity. Their spread is facilitated by native bird species through mutualistic relationships. Studies of seed dispersal of alien invasive plants are important for effective management. In the present study, the role of native bird species in the potential dispersal of a highly invasive shrub *Lantana camara* was investigated. A total of 56 bird species were observed visiting *L. camara* with only 28 species consuming the fruit. Visitation frequencies were significantly higher for small and medium-sized frugivorous species. The dark-capped bulbul *Pycnonotus tricolor* was the frugivorous bird species most observed visiting and is likely the main potential native avian disperser of *L. camara*. Interestingly, two non-frugivorous birds, the white-bellied sunbird *Cinnyris talatala* and the white-browed scrub-robin *Cercotrichas leucophrys* showed relatively high visitation frequencies to *L. camara*. Of the 28 species that ingested fruit, potential dispersal distances ranged from 9 to 45 km. Short dispersal distances were more common than long dispersal distances limited by relatively rare frugivores. Level of frugivory and body size were the main traits that influenced dispersal effectiveness. These results emphasise the importance of evaluating the role of bird species in the dispersal of alien invasive species.

Keywords: avian frugivore, bird- mediated dispersal, fleshy-fruited invasive plant, seed dispersal distance

3.2 Introduction

The spread of alien invasive species especially plants, has become a major problem as it contributes to biodiversity loss worldwide and alters ecosystem functioning (Gooden et al., 2009; Jordaan et al., 2011a, b; Voigt et al., 2011; Carrion-Tacuri et al., 2012; French et al., 2014; Ramaswami et al., 2016; Mungi et al., 2018; Saha et al., 2018; Shackleton et al., 2019). Alien invasions are rated as the second greatest threat to the biodiversity on the natural environment (Jordaan et al., 2011a; Ruwanza and Shackleton, 2016) and are a major component of global change (Ruwanza and Shackleton, 2016; Amodeo et al., 2017; Guzzetti et al., 2017). Their impacts are not only limited to the environment but also negatively affects economies (Jordaan and Downs, 2012; Vardien et al., 2012; Ruwanza and Shackleton, 2016; Lamsal et al., 2018), human well-being (Jordaan et al., 2011a; Vardien et al., 2012; Ruwanza and Shackleton, 2016; Shackleton et al., 2019), and livelihoods (Shackleton et al., 2019; Shrestha et al., 2019). Fleshy-fruited invasive plant species overcome dispersal barriers by forming mutual relationships with frugivores as seed dispersal networks are rarely specialised (Milton et al., 2007; Deckers et al., 2008; Cruz et al., 2013; Ramaswami et al., 2016; Amodeo et al., 2017). These mutual relationships increase the invasion success of fleshy-fruited invasives and have major effects on the structure of plant communities (Aslan, 2011; Jordaan et al., 2011a, b; Jordaan and Downs, 2012; Traveset and Richardson, 2014; Bonilla and Pringle, 2015; Li et al., 2017; Vergara-Tabares et al., 2018; Dlamini et al., 2018). Fleshy-fruited invasive species that are unable to form mutual relationships with native dispersers have reduced invasiveness potential (Aslan, 2011; Aslan and Rejmanek, 2012).

Frugivore-mediated seed dispersal (i.e. the movement and spread of seeds away from their parent plant) of fleshy-fruited invasive plant species is recognised globally (Jordaan et al., 2011; Aslan, 2011; Aslan and Rejmanek, 2012; Vergara-Tabares et al., 2016). Among frugivorous species, avian species have been recognised as most important seed vectors of

plants including facilitating the spread of many fleshy-fruited invasive species (Gosper et al., 2005; Jordaan et al., 2011b; Gleditsch and Carlo, 2011; Corlett, 2017; Li et al., 2017). Birds are important seed dispersers because of their mobility, abundance and high diversity (Gleditsch and Carlo, 2011). Avian seed dispersal begins when frugivorous species consume the fruit and regurgitate or defecate intact seeds in droppings (Jordaan et al., 2011a, b; Thabethe et al., 2015; Camargo et al., 2019). The ecological benefits of avian mediated seed dispersal are the movement of seeds away from the parent plant resulting in reduced competition, mortality and potential deposition of seeds in suitable sites for seed germination (Alan, 2011; Corlett, 2017; Naniwadekar et al., 2019). Avian seed dispersal effectiveness has two main components: qualitative and quantitative (Schupp et al., 2010). Qualitative seed dispersal refers to the probability of a seed surviving and germinating while quantitative takes account of seed removal and visitation rates (Schupp et al., 2010; Rother et al., 2016; Fontúrbel et al., 2017; Gonzalez-Varo et al., 2019). Avian seed dispersal effectiveness varies and is influenced by avian species traits (body size, feeding behaviour and movement patterns) (Amodeo et al., 2017) and plant traits (seed size, crop size). Crop and seed size influences the dispersers selection of the fruit and the trait of the bird species influences the number of fruits that can be consumed per visit and the treatment of the fruit. The pattern of seed dispersal is influenced by the movement patterns of dispersers (Bartuszevige and Gorchov, 2006; Jordaan et al., 2011b; McConkey et al., 2012; Bonilla and Pringle, 2015). Quantifying seed dispersal distance is challenging owing to unpredictable bird behaviour (Mokotjomela et al., 2013a). Despite the difficulties of quantifying dispersal, mechanistic models have been developed to estimate dispersal distances and it has been shown that dispersal distance is affected by several factors such as seed retention time and body mass (Schurr et al., 2009; Tsoar et al., 2011; Mokotjomela, 2013a, 2015). Seed retention time refers to the amount of time a seed is retained within the gut of an avian species (Jordaan et al., 2011; Thabethe et al., 2015; Dlamini et al., 2018). Several

factors influence seed retention time including avian traits (body size) and plant traits (seed size, seed shape) (Khamcha et al., 2014; Yoshiwaka et al., 2019). Amongst these factors, avian body size has suggested as the strongest influencer (Yoshiwaka et al., 2019).

Here, we focused on *Lantana camara* a highly invasive shrub native to Central and Southern America (Niphadkar et al., 2016; Mungi et al., 2018), listed amongst the worst invaders globally (Vardien et al., 2012; Mukwevho et al., 2017) and one of the most prolific invaders in South Africa (Bromilow, 2010; Shackleton et al., 2017; Katembo et al., 2019). In South Africa, the first record of *L. camara* is from 1858 growing in Cape Town, Western Cape Province, while in KwaZulu-Natal Province this alien shrub was introduced as an ornamental plant from Mauritius in ~1883 (Vardien et al., 2012). *Lantana camara* alters the composition, structure and function of natural systems (Sampson et al., 2018) and has allelopathic properties that inhibit the growth of native vegetation (Ruwanza and Shackleton, 2016; Saha et al., 2018). It invades different ecosystems types (Mungi et al., 2018), including forests (Niphadkar et al., 2016; Mungi et al., 2018; Saha et al., 2018; Panda et al., 2018), mangroves, semi-arid areas (Mungi et al., 2018) and pastures (Panda et al., 2018). In South Africa, this highly invasive shrub has invaded over two million hectares and the distribution of the plant is continually increasing because of climatic suitability (Shackleton et al., 2017; Goyal et al., 2018). The most invaded provinces are Mpumalanga, KwaZulu-Natal and Eastern Cape (Ruwanza and Shackleton, 2016). The ability of *L. camara* to integrate into local seed dispersal networks is amongst the factors that have contributed to its spread (Shackleton et al., 2017). Despite the knowledge of *L. camara* forming mutual relationships with native dispersers, in South Africa, the assemblage of avian species dispersing the seeds of this plant remains unknown (Taylor et al., 2018).

South Africa has been extensively invaded by fleshy-fruited invasive plant species

(Thabethe et al., 2015). Presently, there is relatively limited information of the role that birds play in effective seed dispersal of alien invasive species and dispersal distances, especially in southern Africa (Mokotjomela et al., 2013a, b, 2015). Considering the impacts of invasive plant species, it is important to understand the ecological processes that are leading to their successful spread and establishment for effective management and biodiversity conservation (Murray and Philipps, 2010; Ramaswami et al., 2016; Amodeo et al., 2017; Dlamini et al., 2018). Long established invasive plant species need different management strategies to newly introduced species, that will ensure that the populations of the plant are maintained at low population densities to minimise ecological and socio-economic impacts. Despite the importance of the mutual relationship of invasive plants with native dispersers, these interactions remain rarely considered in management. Our main aim of the present study was to understand the contribution of avian species in the dispersal of *L. camara* seeds. Our objectives were to determine (1) avian species that were dispersing *L. camara* seeds and (2) potential dispersal distances that ingested seeds were dispersed over. We predicted that *L. camara* would benefit from generalist avian species for potential seed dispersal services.

3.3 Materials and Methods

3.3.1 Plant species

Lantana camara varies morphologically and there are about 50 varieties in South Africa alone (Bromilow, 2010; Vardien et al., 2012) but all considered to be one species (Bromilow, 2010). The flowers vary in colour and can either be white, yellow, orange, pink or red in one flat-topped head (Henderson, 1995). The fruits of *L. camara* are relatively small (Bromilow, 2010) made up of shiny black drupes with a diameter of ~5 mm (Venkatachalam et al., 2011) and seed size ~ 3 mm (Jordaan et al., 2011).

3.3.2 Study sites

The study was conducted at two sites in KwaZulu-Natal Province, South Africa. The first site, Fountain Hill Estate (29.4470 S, 30.5461 E) a ~2200 ha privately owned game reserve and commercial farm located outside of Wartburg, ~30 km from Pietermaritzburg. The property is bordered by sugarcane plantations and about 1600 ha has been maintained naturally for wildlife (Grey-Ross et al., 2009). The site has a mean annual precipitation of 805 mm, 3.3 °C minimum mean temperature and 37.4 °C maximum mean temperature (Musokwa et al., 2019). Most rainfall is received in January and June is the driest month of the year (Chibarabada et al., 2018) and the bird community comprises a total of 273 bird species (E. Gevers, pers. comm.). The wooded grassland areas within the reserve have been encroached by woody species and alien invasive species (pers. obs.). The second site, Ukulinga Research Farm (29.6627 S, 30.4050 E) is the research farm of the University of KwaZulu-Natal near Pietermaritzburg. It has a mean annual precipitation 694-850 mm received between October and April and is dominated by tall grassveld (Akinnuoye-Adelabu et al., 2019) and *Vallechia* trees (previously *Acacia*). Ukulinga Research Farm *L. camara* infestations are established under *Vallechia* trees (previously *Acacia*) and at Fountain Hill Estate the plant has formed dense, impenetrable thickets in the landscape (pers. obs.).

3.3.3 Study sampling

Reproductively matured shrubs of *L. camara* were selected and observed for two consecutive years (2017/2018) at Fountain Hill Estate during its fruiting season. We added Ukulinga Research Farm in 2018 as an additional site and observed fruiting shrubs for a total of 58 h to understand if the same species were contributing to the dispersal of *L. camara*. Observations were alternated between four observational points that were randomly selected in both sites.

Lantana camara has formed thick clusters in both selected sites. Therefore, observations were conducted on a cluster of two to three tree at a time. Trial observations were conducted and showed that birds foraged throughout the day. Hence, observations were conducted from 06:00 am to 17:30 pm each day. Observations were performed manually by two observers with binoculars (Ultra optec, 8X40 magnification, fully coated optics) approximately 30 m away from the shrubs. For each bird visitation, the time of the day, bird species, the number of species observed and fruit-seed handling behaviour (pecking, swallowing, dropping fruit/seed under the parent plant and removing the fruit away from the tree) was recorded. All feeding was observed Bird species were identified by the keys and descriptions presented in Chittenden et al. (2007).

3.3.4 Data synthesis and analyses

Observed bird species were divided into functional groups for analyses. These groupings were based on their body mass and proportion of fruit in their diet. Observed bird species were classified into four body-size groups defined by Moran et al. (2004): relatively large birds (> 150 g), medium size (50 –150 g), small birds (30 –50 g), and relatively very small birds (< 30 g). Recorded bird species were categorised into three main frugivore classes: highly frugivorous birds that depend mainly on the fruit as their source of food, moderately frugivorous birds with fruit as their secondary source of food, and non-frugivorous birds that have their diet associated with the fruit of the alien plants (insects, nectar). To gather information on the body mass and diet composition of species we used Hockey et al. (2005). To estimate the dispersal distance of all bird species that were observed consuming *L. camara* fruits, seed retention time and flight speeds were calculated using established equations (Schurr et al., 2009; Tsoar et al., 2011; Mokotjomela et al., 2013a) as follows:

$$\text{SRT} = 1.6 (\text{BM})^{0.33}$$

where SRT is the seed retention time (h), BM body mass in (kg) and 0.33 and 1.6 allometric constants.

$$\text{FS} = 15.7 (\text{BM})^{0.17}$$

where FS is flight speed (m.s^{-1}), body mass (kg) and 15.7 and 0.17 were allometric constants.

We acknowledge that these metrics do not take into consideration the behaviour of individual bird species post-feeding, as such, we present the results of potential dispersal distances as maximum potential dispersal distances for each species, cognisant that individual behaviours may reduce the actual dispersal distance.

The data were analysed using the General Linear Model Repeated Measures Analysis of Variance (ANOVA). Post-hoc tests were used for further investigation where significant differences were evident. The first analysis of variance was performed to test differences in visitation frequencies of birds of different sizes. We then tested for differences in visitation frequencies of birds in the different frugivore classes. This was followed by analyses of differences in visitation frequency of birds at different times of the day. All statistical analyses were conducted using STATISTICA (Statsoft, Tulsa, OK).

3.4 Results

During the total of 268 h of observations of the *L. camara*, there was a total of 517 total observations of 56 native bird species visiting the *L. camara* shrubs (Table S3.1). However, only 28 species fed on the fruit (Table S3.2). Of the total of 28 avian species observed consuming the *L. camara* fruits (Table S3.1), some of the species (doves, finches, canaries, and weavers) were granivorous species. Most frugivorous birds (62 %) that consumed the *L. camara* fruits flew onto a nearby *Vachellia* species (previously *Acacia spp.*) tree, 4 % dived to

the ground, 12% flew onto another *L. camara* shrub and 22 % flew out of sight from the area. The dark-capped bulbul (*Pycnonotus tricolor*) had the highest visitation frequency of all frugivores in both sites with a total of 108 observations throughout the study. The two study sites differed in species composition observed visiting *L. camara*. At Fountain Hill Estate, most common avian visitors after the dark-capped bulbul were two moderately frugivorous species the Cape white-eye (*Zosterops virens*) and African firefinch (*Lagonosticta rubricata*), and one highly frugivorous species the speckled mousebird (*Colius striatus*). At Ukulinga it was the speckled mousebird and two moderately frugivorous species the common fiscal (*Lanius collaris*) and the fiscal flycatcher (*Sigelus silens*). Dark-capped bulbuls were often observed feeding in pairs, while Cape white-eyes and speckled mousebirds, were often in small flocks at a time. The white-bellied sunbird (*Cinnyris talatala*) and white-browed scrub robin (*Cercotrichas leucophrys*) were the most frequent non-frugivorous bird species observed visiting *L. camara* for either nectar or insects.

The most abundant and common native avian visitors to the *L. camara* shrubs were relatively small bird species (Fig. 3.1). The purple-crested turaco (*Tauraco porphyreolophus*) was the only large frugivore observed feeding on *L. camara* throughout the study (Table S3.2). Visitation frequency varied differently between birds of different body mass (ANOVA: $F_{2, 14} = 4.7987$, $n = 8$, $p = 0.02587$). The visitation frequency for relatively small birds was (6.3 ± 0.7 , 8.9 ± 0.9) and significantly higher than medium-sized birds and small birds in 2017 and 2018 (Turkey HSD: $p = 0.000174$, 0.000190 respectively, Fig. 3.1). There were significant differences in visitation frequencies at different times of the day (ANOVA: $F_{3, 18} = 5.1058$, $p = 0.00989$). Visitation frequency was significantly higher in the early mornings than in the afternoon in 2018 (Turkey HSD: $p = 0.001343$, Fig. 3.2). Visitation frequency varied significantly different between the three frugivory classes ($F_{2, 14} = 6.5630$, $p = 0.00975$). The

visitation frequency by moderately frugivorous birds was significantly higher than non-frugivorous birds in both 2017 and 2018 (Turkey HSD: $p = 0.040, 0.002$ respectively, Fig. 3.3).

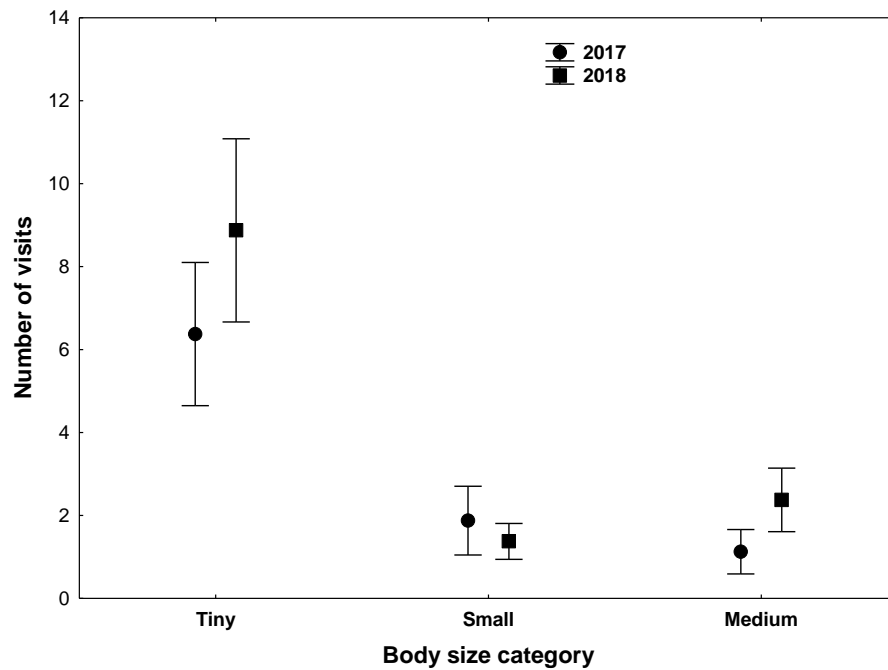


Fig 3.1. Visitation frequency by bird species of different body mass to *Lantana camara* shrubs ($n = 8$). (The error bars indicate the mean \pm S.E. of visitation frequency for three of the four body size categories. Large was omitted as only one species was observed.)

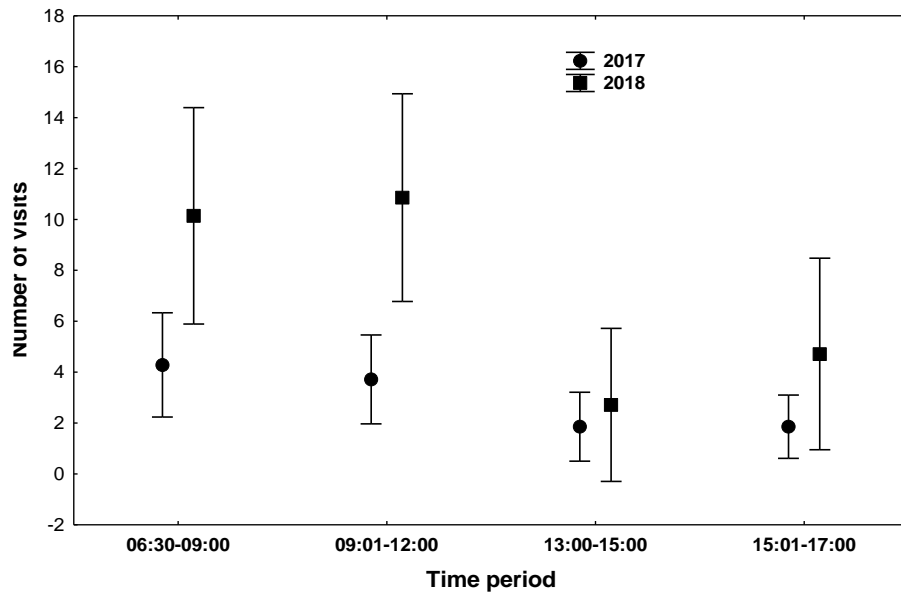


Fig 3.2. Visitation frequency to *Lantana camara shrubs* by different bird species at different times of the day (n = 8) in the present study. (The error bars indicate the mean \pm S.E. of number of visits for the four time periods).

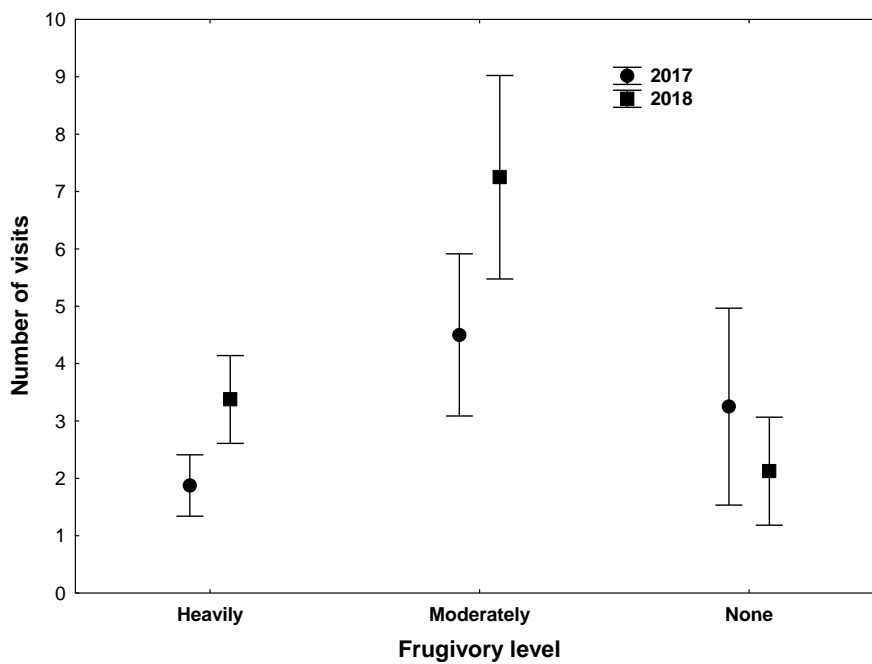


Fig 3.3. Visitation frequency by bird species of different frugivory level (Table 3.1) observed visiting *Lantana camara shrubs* (n = 8) in the present study. (The error bars indicate the mean \pm S.E. of visitation frequency for three frugivory level).

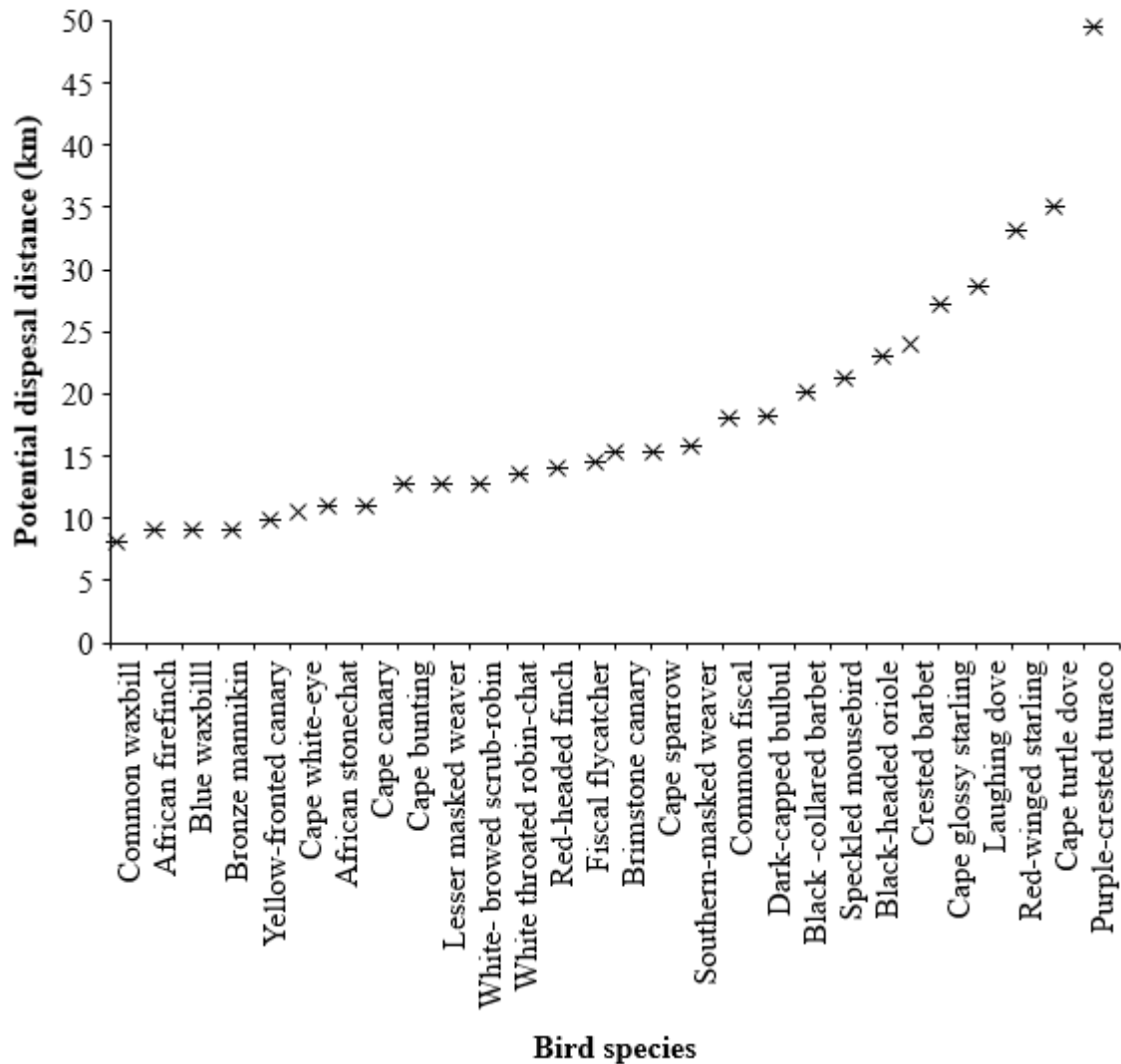


Fig 3.4. Potential dispersal distance of *Lantana camara* seeds ingested by frugivorous birds in KwaZulu-Natal, South Africa in the present study.

3.5 Discussion

Observations of native bird species visiting *L. camara* showed that many native bird species were interacting with the shrub and used it either as a food source or for perching, or both. These results are consistent with previous studies that showed that invasive species interact with multiple bird species (Corlett, 2005; Buckley et al., 2006; Taylor et al., 2018;

Thibault et al., 2018 a, b,c) and are potentially dispersed by a range of bird species. Similarly, in India where *L. camara* is highly invasive, it was associated with increased abundance of insectivores, nectivores and frugivores (Aravind et al., 2010). The high visitation frequency of the tawny-flanked prinia (*Prinia subflava*) in the present study may have been a result of the high abundance of invertebrates that are reported to be associated with this invasive plant species (Corlett, 2005). *Lantana camara* is a competitor for pollinators (Bhagwat et al., 2012) and produces large amounts of nectar (Aravind et al., 2010) and this could explain the high visitation by the White-bellied Sunbird. The presence of pollinators also contributes to the success of *L. camara* as they account for the high fruit produced (Sharma et al., 2005). As much as non- frugivorous birds may have effects on seed dispersal, these are not comparable to the effects by frugivorous birds (Dennis, 2007; Heleno et al., 2013). Therefore, avian seed dispersers of *L. camara* varied and ranged from effective to non-effective seed dispersers depending on the frugivory level of the species.

In this study, dark-capped bulbuls had the highest visitation frequency at both sites, suggesting that this species was potentially the main disperser of *L. camara*. In a previous study in India, bulbuls (*Pycnonotus* spp.) were also the main disperses of *L. camara*, as the abundance of two frugivorous bulbuls, red-vented bulbul (*P. cafer*) and white-browed bulbul (*P. uteolus*) increased significantly with an increase in *L. camara* abundance (Araving et al., 2010). Fruits of *L. camara* are particularly important for dark-capped bulbul as they meet their daily energy requirements (Jordaan et al., 2011a). Bulbuls generally consume more *L. camara* fruits than other frugivores (Araving et al., 2010; Ramaswami et al., 2016) and are often dependent on the fruit (Spiegel and Nathan, 2007). In the present study, they were observed feeding either in pairs or small flocks and that likely resulted in high seed removal rates. Dark-capped bulbuls fly across open habits between fruiting and resting trees (Voigt et al., 2011) and often swallow fruit whole leaving seeds undamaged (Corlett, 2005; Corlett, 2017).

Consequently, ingested seeds had a high potential of being dispersed into suitable microsites and germinating. This is mainly because small birds, dark-capped bulbul in this case perch for fruit processing and will likely drop seeds in woody microhabitat that provide moisture and favour the germination ecology of *L. camara*. Propagulate pressure for a species like *L. camara* that can vegetatively reproduce and has a persistent seed bank adds to the magnitude of invasiveness and colonization (Gentle and Duggin, 1997; Totland et al., 2005). Thus, we concluded that dark-capped bulbuls were important quantitatively as effective potential dispersers of *L. camara*.

The most abundant and common native avian visitors to *L. camara* shrubs were relatively small, moderately frugivorous bird species. This reflects the ability of generalist species to incorporate a new food source in their diet. Similarly, other studies have shown that fleshy-fruited invasive plant species are dispersed by small-sized generalist frugivores (Jordaan et al., a, b, 2011, Amodeo et al., 2017). Fleshy-fruited invasive species promote the persistence of generalist species as some non-frugivorous avian species can switch diet and supplement with fruit when their primary diet is limited (Gleditsch, 2017). Frugivorous birds with the highest visitation frequencies differed across the two sites in this study. The differences were the species composition assemblage but the traits affecting seed dispersal (e.g body size, level of frugivory) were not different. Our data did not allow for a multi-site comparison as the second site was observed for a relatively short time. Despite this, our results suggested differences in avian species composition in different habitats. A comparative study by Bleher and Bohning-Gaese (2001) showed that regional differences in species diversity do not only affect dispersal but the distances seeds can be dispersed over and establish.

Most of the observed avian frugivores that consumed *L. camara* seeds flew into *Vachellia* trees. Post-foraging behaviour needs to be considered to determine the complexity of seed dispersal (Dennis, 2007). *Lantana camara* is an understory species (Avarind et al.,

2010) and the dispersed seeds had an increased chance of germinating as canopy cover provides conditions that facilitate establishment (Buckley et al., 2006; Spiegel and Nathan, 2007). Therefore, habitat structure plays an important role in the success of alien invasive species (McConkey et al., 2004; Gosper et al., 2005; Buckley et al., 2006). Survival chances are further enhanced by prickles of *L. camara* as they discourage browsing (Vardien, et al. 2012).

The high number of avian frugivores observed feeding many have been a result of the fruit characteristics of *L. camara*. Invaders with relatively small seeds (Buckley et al., 2006; Gosper and Vivian-Smith, 2010; Jordaan et al., 2011a) and those with single seeds (Jordaan et al., 2011a,b) attract a range of bird species and are associated with high probability of fruit removal and dispersal (Herrera, 1984; Corlett 1998; Bleher and Bohning-Gaese 2001; Gosper et al., 2005). The size of the fruit interacts with bird traits (gape width) and determine if the fruit can be swallowed whole or pecked (Corlett, 1998; Jordano, 2000; Symes and Downs, 2001). The small seeds of *L. camara* are a likely advantage for the plant to be a successful invader as the fruit size accommodated all gape widths of all species observed. Additionally, a relatively high number of shrubs had ripe fruits at the end of the fruiting season of many native plants (per. obs.). Fleshy-fruited invasive species produce a high fruit set to integrate into local dispersal networks when native fruiting trees are out of fruit and avian species are exposed to low food availability (Martin-Albarracin et al., 2018). Some avian species observed feeding on *L. camara* were seed predators (e.g. weavers (Ploceidae), canaries (Fringillidae), finches (Estrilidae) and doves (Columbinidae) rendering them as ineffective disperses. Therefore, fruit ingestion does not always lead to successful dispersal. It is important to note that the visitation frequency of granivorous species was low, therefore a large proportion of seed escaped predation. In addition, the damage by the predatory species was likely minimal as *L. camara* produces large crop size (pers. obs.).

Estimated potential dispersal distances were relatively longer than normally predicted distances. Similarly, other studies (McConkey et al., 2004; Mokotjomela et al., 2013b; Viana et al., 2013) have shown longer dispersal distances up to 100 km. Theoretically, these distances are possible, although bird behaviour is likely to limit the maximum distance. However, it is not possible to quantify this behaviour here, as the birds were untracked and therefore it was not possible to monitor their behaviour post-feeding, and detailed activity budgets for the avian community recorded here are not available to consider time not spent travelling. Therefore, we expect the predicted maximum seed-dispersal distances to be shorter when considering bird behaviour (i.e. resting, further feeding, social interactions) post-feeding. For example, Kays et al. (2011) estimated relatively short distance (144 m – 147 mm) using high resolution locations and accelerometer that accounted for the bird behavior. Similarly, Wotton and Kelly (2012) showed estimated relatively short distances. Despite the limitation of allometric based model they are essential in understanding seed dispersal patterns to contribute to conservation especially in the context of alien invasive plant mutualism with native dispersers (Yoshiwaka et al., 2019). Considering the number of native avian species that ingested the seed of *L. camara* were generally small sized with relatively shorter seed retention time, this likely reduced seed dispersal distances and will result in local dense infestations in both sites.

3.5.1 Conclusions

The primary goal of this study was to determine the avian species assemblage that is dispersing *L. camara* seeds. Focal observation on fleshy-fruited invasive plant species is important and it provides an opportunity of understanding invasion dynamics. Native bird species interacted with *L. camara* and played a role in the dispersal of *L. camara* seeds. Also, the results suggested that *L. camara* was more effectively dispersed by relatively small-sized native bird species compared with large relatively rare frugivores, based on visitation rates and abundance.

Effectiveness of dispersal of *L. camara* depends largely on the traits of the bird species (level of frugivory, body size, gape width, movement strategy) visiting the plants in an area, hence, the role of native frugivores in the potential dispersal of *L. camara* is likely to vary geographically as it depends on the local native bird species. Therefore, to manage invasive species in an area the composition of native bird species must be assessed to consider the potential dispersal distances. Management of fleshy-fruited invasive plant species is complex. Therefore, the management of *L. camara* needs adaptive approaches as complete eradication of this invasive shrub have been shown to be difficult (Bhagwat et al., 2012; Ramaswami et al., 2016). For example, if *L. camara* is being eradicated, native fleshy fruiting species should be established to provide native bird species with a native alternative food source. For conservation purposes, it is important to raise public awareness of the importance of planting fleshy-fruited native trees for various avian frugivores, that are functionally equivalent to *L. camara* such as *L. rugosa*. Finally, we recommend that future research investigates the role mammal frugivores in the dispersal of fleshy-fruited invasive plant species such as *L. camara* as some of these were observed feeding on the fruit during our study (NB unpublished data).

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3.8 Supporting information

Table S3.1 Bird species observed visiting *Lantana camara* at Ukulinga Research farm (URF) and Fountain Hill Estate (FHE), KwaZulu-Natal Province, South Africa.

Bird species	Scientific name	Primary diet	Visited	Ingested fruit	Site
African firefinch	<i>Lagonosticta rubricata</i>	Granivory	✓	✓	FHE
African hoopoe	<i>Upupa africana</i>	Insectivory	✓	-	URF
African pied wagtail	<i>Motacilla aguimp</i>	Insectivory	✓	-	URF
African pygmy kingfisher	<i>Ispidina picta</i>	Insectivory	✓	-	FHE
African stonechat	<i>Saxicola torquatus</i>	Insectivory	✓	✓	FHE and URF
Bar throated apalis	<i>Apalis thoracica</i>	Insectivory	✓	-	FHE
Black-collared barbet	<i>Lybius torquatus</i>	Frugivory	✓	✓	FHE
Black-crowned tchraga	<i>Tchagra senegalus</i>	Insectivory	✓	-	FHE and URF
Black-headed oriole	<i>Oriolus larvatus</i>	Omnivory	✓	✓	FHE
Blue waxbill	<i>Ureaginthus angolensis</i>	Granivory	✓	✓	FHE
Brimstone canary	<i>Crithagra sulphurata</i>	Frugivory/ granivory	✓	✓	FHE
Bronze manikin	<i>Spermestes cucullata</i>	Granivory	✓	✓	FHE
Brown hooded kingfisher	<i>Halcyon albiventris</i>	Insectivory	✓	-	FHE
Cape batis	<i>Batis capensis</i>	Insectivory	✓	-	FHE
Cape bunting	<i>Emberiza capensis</i>	Granivory	✓	✓	FHE and URF
Cape canary	<i>Serinus canicollis</i>	Granivory	✓	✓	FHE
Cape glossy starling	<i>Lamprotornis nitens</i>	Frugivory	✓	✓	FHE
Cape robin chat	<i>Cossypha caffra</i>	Insectivory	✓	-	FHE and URF
Cape sparrow	<i>Passer melanurus</i>	Granivory	✓	✓	URF
Cape turtle dove	<i>Streptopelia capicola</i>	Granivory	✓	✓	FHE
Cape white-eye	<i>Zosterops virens</i>	Omnivory	✓	✓	FHE
Chinspot batis	<i>Batis capensis</i>	Insectivory	✓	-	URF
Common fiscal	<i>Lanius collaris</i>	Insectivory	✓	✓	URF
Common scimitarbill	<i>Rhinopamastus purpureus</i>	Insectivory	✓	-	FHE

Common waxbill	<i>Estrilda astrild</i>	Granivory	✓	✓	FHE
Crested barbet	<i>Trachyphonus vaillantii</i>	Omnivory	✓	✓	FHE
Croaking cisticolla	<i>Cisticola natalensis</i>	Insectivory	✓	-	FHE
Dark-capped bulbul	<i>Pycnonotus tricolor</i>	Frugivory	✓	✓	FHE and URF
Fiscal flycatcher	<i>Sigelus silens</i>	Insectivory	✓	✓	FHE and URF
Levaillant's cisticolla	<i>Cisticola tinniens</i>	Insectivory	✓	-	FHE
Laughing dove	<i>Streptopelia senegalensis</i>	Granivory	✓	✓	FHE and URF
Lazy cisticolla	<i>Cisticola aberrans</i>	Insectivory	✓	-	FHE
Lesser masked weaver	<i>Ploceus intermedius</i>	Insectivory	✓	✓	FHE
Little bee-eater	<i>Merops pusillus</i>	Insectivory	✓	-	FHE
Little rush warbler	<i>Bradypterus baboecala</i>	Insectivory	✓	-	URF
Long-billed crombec	<i>Sylvietta rufescens</i>	Insectivory	✓	-	URF
Malachite sunbird	<i>Nectarinia famosa</i>	Nectivory	✓	-	FHE
Neddicky	<i>Cisticolla fulvicapilla</i>	Insectivory	✓	-	FHE
Purple-crested turaco	<i>Tauraco porphyreolophus</i>	Frugivory	✓	✓	FHE
Red capped robin chat	<i>Cossypha natalensis</i>	Insectivory	✓	-	FHE
Red-headed finch	<i>Amadina erythrocephala</i>	Granivory	✓	✓	URF
Red-winged starling	<i>Onychognathus morio</i>	Frugivory	✓	✓	FHE
Rufous-napped lark	<i>Mirafra africana</i>	Insectivory	✓	-	FHE
Southern black tit	<i>Parus niger</i>	Insectivory	✓	-	FHE
Southern black flycatcher	<i>Melaenornis pammelaina</i>	Insectivory	✓	-	FHE
Southern boubou	<i>Laniarius ferrugineus</i>	Insectivory	✓	-	FHE
Southern masked weaver	<i>Ploceus velatus</i>	Granivory	✓	✓	FHE
Speckled mousebird	<i>Colius striatus</i>	Frugivory	✓	✓	FHE and URF
Spectacled weaver	<i>Ploceus ocularis</i>	Insectivory	✓	-	FHE
Swee waxbill	<i>Coccygia melanotis</i>	Granivory	✓	-	FHE

Tawny flanked prinia	<i>Prinia subflava</i>	Insectivory	✓	-	FHE
White-bellied sunbird	<i>Cinnyris talatala</i>	Nectivory	✓	-	FHE
White-browed scrub robin	<i>Cercotrichas signata</i>	Insectivory	✓	✓	FHE and URF
White-throated robin chat	<i>Cossypha humeralis</i>	Insectivory	✓	✓	FHE
Yellow-fronted canary	<i>Crithagra mozambica</i>	Granivory	✓	✓	FHE
Yellow-throated petronia	<i>Petronia supercilialis</i>	Insectivory	✓	-	FHE

Table S3.2 Calculated variables for modelling potential dispersal distance of 28 native frugivorous bird species observed ingesting the fruit of *L. camara* in the present study

Bird species	Common name	Body mass (kg)	Seed retention (min)
African firefinch	<i>Lagonosticta rubricata</i>	0.01	1260.2
African stonechat	<i>Saxicola torquatus</i>	0.02	1440.6
Black-collared barbet	<i>Lybius torquatus</i>	0.05	2143.3
Black-headed oriole	<i>Oriolus larvatus</i>	0.07	2337.1
Blue waxbill	<i>Uraeginthus angolensis</i>	0.01	1260.2
Brimstone canary	<i>Crithagra sulphuratus</i>	0.03	1790.7
Bronze mannikin	<i>Lonchura cucullata</i>	0.01	1260.2
Cape bunting	<i>Emberiza capensis</i>	0.02	1584.0
Cape canary	<i>Serinus canicollis</i>	0.02	1440.6
Cape glossy starling	<i>Lamprotornis nitens</i>	0.09	2602.1
Cape sparrow	<i>Passer melanurus</i>	0.03	1790.7
Cape turtle dove	<i>Streptopelia capicola</i>	0.15	3079.9
Cape white-eye	<i>Zosterops virens</i>	0.01	1391.3
Common waxbill	<i>Estrilda astrild</i>	0.01	1170.7
Common fiscal	<i>Lanius collaris</i>	0.04	1991.1
Crested barbet	<i>Trachyphonus vaillantii</i>	0.07	2395.0
Fiscal flycatcher	<i>Sigelus silens</i>	0.03	1727.3
Laughing dove	<i>Streptopelia senegalensis</i>	0.10	2694.2
Dark-capped bulbul	<i>Pyconotus tricolor</i>	0.04	1996.9
Lesser masked weaver	<i>Ploceus intermedius</i>	0.02	1584.0
Purple-crested turaco	<i>Tauraco porphyreolophus</i>	0.30	3871.4
Red-headed finch	<i>Amadina erythrocephala</i>	0.02	1682.3
Red-winged starling	<i>Onychognathus morio</i>	0.14	2974.6
Southern masked weaver	<i>Ploceus velatus</i>	0.03	1818.1
Speckled mousebird	<i>Colius striatus</i>	0.06	2211.8
White-browed scrub robin	<i>Cercotrichas leucophrys</i>	0.02	1584.0
White-throated robin chat	<i>Cossypha humeralis</i>	0.02	1646.8
Yellow-fronted canary	<i>Serinus mozambicus</i>	0.01	1338.3

CHAPTER 4

A global impact assessment of alien invasive fleshy-fruited plants generally dispersed by native avian species in South Africa

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Running header: Impact assessment of fleshy-fruited invasive plant species

4.1 Abstract

Aim: Alien invasive plant species have been identified as a major threat to biodiversity and the relationship with avian dispersers increases their invasiveness potential. The impact of invasive plant species needs to be quantified using assessment tools that are comparable across different habitats and species in order to allocate limited resources to high priority species. Here, we assessed the environmental and economic impacts of fleshy-fruited invasive plant species in South Africa to guide resource allocation and prevent further uncontrolled introductions.

Location: Global

Methods: The generic impact scoring system was used to assess the socio-economic and environmental impacts of 16 fleshy-fruited invasive species that are listed in South Africa. We investigated the difference in the impact, impact mechanisms and the number of papers used for each species.

Results: The results showed that fleshy-fruited invasive species have both environmental and socio-economic impacts. The overall impact scores for *Lantana camara* and *Ailanthus altissima* were the highest with scores of 46 and 32, respectively. Some species, such as *Morus alba*, *Cinnamomum camphora*, *Rubus cuneifolius* and *Schinus terebinthifolius* had a low overall impact scores of 8, 18, 14 and 16, respectively but scored the maximum impact score of 5 for certain mechanisms. Environmental impacts were mainly through ecosystem and vegetation while socio-economic impacts were through forest production, agriculture, and human health.

Main conclusion: Fleshy-fruited invasive plant species pose economic and socio-economic impacts. The information generated in this study is important for guiding resource allocation and prevention of uncontrolled introduction of invasive species in South Africa. The impact of the fleshy fruited invasive species transcended sectors and therefore, effective management of invasive species will require the collaboration of multiple and inter-sectoral stakeholders in South Africa.

Keywords

alien invasive plants, environmental impacts, GISS, impact score, socio-economic impacts

4.2 Introduction

Biodiversity is important as it serves several ecosystem services and should thus be managed sustainably. However, occasionally local ecosystems are invaded by invasive species, which threaten the natural balance and pose numerous management hurdles. Invasive species are defined as species of plants that proliferate uncontrollably in a given environment to the detriment of other species and pose a threat to socio-economic welfare of the surrounding communities (Russel & Blackburn, 2017). Globally, biological invasions have been identified as a major threat to biodiversity (Henderson & Wilson, 2017; Ahmad et al., 2019a; Mofu et al., 2019), the functioning of ecosystems and human livelihoods (Early et al., 2016; Pratt et al., 2017). Ecosystem services such as nutrient cycling, hydrological process and land suitability can be disrupted by over dominance by a single or numerous invasive species that proliferate at the expense of other species. There are several factors that promote proliferation of invasive species. Alien invasive plant species are either introduced accidentally or intentionally for recreation (van Wilgen et al., 2008), forestry, agriculture, horticulture (Arriaga et al., 2004; van Wilgen et al., 2008; Kumschick et al., 2012), restoration (Kumschick et al., 2012) and ornamentals (Hulme et al., 2018; Verbrugge et al., 2019). New introductions or movements of alien invasive plant species within a country are promoted by increased domestic and global travel and trade making their management a challenge in many countries (Leung et al., 2012; Early et al., 2016; Padayachee et al., 2019; Seebens, 2019). The spread of alien invasive plant species is further exacerbated by the change in global climate (Ahmad et al., 2019a, b; Mofu et al., 2019).

Shifts in global temperatures and rainfall can promote the invasiveness of a species. In some cases, the temperature or rainfall can suppress the growth of a species making an otherwise non-invasive species to become invasive. Abandonment of land previously used for agriculture because of climate change can promote proliferation of invasive species benefitting from residual high nutrition and lack of land management. Alien invasive species impact biodiversity in several ways and the effects can be far reaching. Depending on the species, alien invasive plants generally reduce species richness (Gaertner et al., 2009; Pyšek et al., 2012), disrupt pollination and dispersal networks (Pyšek et al., 2012), change ecosystem functioning (Andersen et al., 2004; Charles & Dukes, 2008; Vilà et al., 2011; Novoa et al., 2016), cause economic losses (Novoa et al., 2016; Zengeya et al., 2017), and impact human well-being (Vilà et al., 2011). Species richness is reduced when an alien invasive species dominates in an ecosystem to the detriment of other species. This can result in complete or partial replacement of other species by the single dominant species. Human well-being is impacted when invasive species reduce quantity or quality of agricultural produce or affect the aesthetic beauty of the environment with adverse effects on economic value or tourism.

South Africa, like other parts of the world, is severely affected by alien plant invasion (Nel et al., 2004; Gaertner et al., 2009; Henderson & Wilson, 2017; Walker et al., 2017; McLean et al., 2018). Alien invasive plant species cover about 80 000 km² (SANBI, 2017) and are continually increasing at an alarming rate (Henderson & Wilson, 2017). In 2010, there were almost 9000 introductions of which 559 were invasive and 660 naturalised (Walker et al., 2017). The widespread disruption of ecosystems by alien invasive species has become a national concern in South Africa because of their impact. The South African government invests over ZAR 1.5 million a year in managing alien invasive plants (SANBI, 2017) and the limited budget dictates management strategies and species to be controlled

(Nel et al., 2004). While progress has been made by the government to control alien invasive plants, it is still unknown if the top priority plant species are being targeted (van Wilgen et al., 2012; Moshobane et al., 2019). One of the most damaging and widespread species is the fleshy-fruited species, which include *Lantana camara* and *Ailanthus altissima*. Fleshy-fruited invasive species are identified by their fruits that are juicy and often sweet and attractive to birds, making them easily dispersed (Jordaan et al., 2011). Fleshy-fruited invasive plant species are a major problem and the mutual relationship with seed dispersers is a key component for their success (Gosper & Vivian-Smith, 2009; Voigt et al., 2011; Thabethe et al., 2015).

The impact of alien invasive plant species varies amongst different species (Blackburn et al., 2014; Schirmel et al., 2016). Despite the growing number of studies reporting the impacts of alien invasive species, there is still a lack of quantitative synthesis of the impacts. Quantifying the impact of different species will aid in listing of species based on their impacts and help in formulating regional and national management strategies (Nel et al., 2004; McGeoch et al., 2012; Novoa et al., 2016; Moshobane et al., 2019). Listing has significant political and economic consequences (Andersen et al., 2004; Wilson et al., 2013; Henderson & Wilson, 2017) and often complicated by balancing the damages and benefits offered by the alien invasive plants (Andersen et al., 2004; Henderson & Wilson, 2017). This highlights the importance of standardised (Nentwig et al., 2016; White et al., 2019), evidence-based and transparent methods like impact assessment tools (Wilson et al., 2013; Nentwig et al., 2016). Impact assessment tools assist in understanding the magnitude and scope of impacts based on the impacts posed by species elsewhere (Kumschick et al., 2014; 2015). Risk impact assessment is a cost-effective tool (Nkuna et al., 2018) and it strengthens the understanding of impacts associated with newly introduced and well-established alien invasive species (Andersen et al., 2004). This quantitative assessment is comparable across different species and habitats

(Kumschick et al., 2014, 2015; Nentwig et al., 2016), integrates ecological and socio-economic impacts (Andersen et al., 2004) and help prioritise limited resources to manage species (Nentwig et al., 2016; Nkuna et al., 2018). Acknowledging the impacts of alien invasive species, the South African government listed alien invasive species into different categories based on expert knowledge for legislation (SANBI, 2017). This process took a period of nine years complicated by conflicting ideas between stakeholders, the difficulty in recruiting experts and changes in project coordinators (Moshobane et al., 2019). Listing of alien invasive species based on expert opinion is often subjective (McGeoch et al., 2012; Turbe et al., 2017; Verbrugge et al., 2019). Hence, a comprehensive risk assessment of non-native trees and shrubs is still lacking in South Africa (Wilson et al., 2013; Clusella & Garcia, 2017). Limitations of the expert-based listing is that: (1) the impact scores are not comparable across habitats and (2) there is no objective criterion that determines if a score is enough for a species to qualify as a high priority. In addition, there is a need to investigate both ecological and economic impacts of alien species as most studies have only focused on either ecological or economic impacts (Jeschke et al., 2014).

As part of the global biodiversity goals, most countries around the world are committed to prevent the introduction of high priority species or minimise their impacts (Moshobane et al., 2019; Verbrugge et al., 2019). The Department of Environmental Affairs (DEA) through the South African National Biodiversity Institute (SANBI) aims to eventually conduct a risk assessment for all listed species. Of the 379 listed terrestrial invasive plant species (DEA, 2016) only 75 plants species have been assessed. Assessing the impacts posed by listed species is important to ensure that all listed species pose a threat so that the listing can be challenged (SANBI, 2017). In responding to the information needs of policymakers, the present study aimed to assess ecological and socio-economic impacts posed by listed fleshy-fruited invasive plant species dispersed by native avian species in

South Africa. Fleshy-fruited invasive plant species are a major problem in South Africa and their spread is mainly facilitated by frugivorous bird species ((Richardson & van Wilgen, 2004; Jordaan & Downs, 2012; Thabethe et al., 2015; Dlamini et al., 2018). The results from this study will assist in informing decision making and in the allocation of resources to control alien plant species. Also, where the study species have not yet been introduced it will help guide decisions around permitting or prohibiting activities.

4.3 Methods

4.3.1 Species selection and literature search

Sixteen fleshy-fruited invasive trees and/or shrubs that are listed under the South African National Environmental Management; Biodiversity Act (NEMBA) were selected for this study. Among the NEMBA listed fleshy fruited species, the species that are most dispersed by native avian species were selected. A literature survey based on published scientific literature and e-literature from Google Scholar (<https://scholar.google.com>) and Web of Science – ISI Web of Knowledge (<https://apps.webofknowledge.com>), and the global invasive species database such as the Global Invasive Species Database (GISD: www.iucngisd.org/gisd) and the Invasive Species Specialist Group (ISSG: www.iucngisd.org/gisd) was conducted prior to assess the risk posed by the species. Synonyms of the species were used to search for the literature and filter the search by the information provided on the abstracts and titles. In addition, we used a combination of terms such as “alien invasive plants”, “ecological impacts”, “economic impacts”, “negative impacts” to search for papers. All the references of the selected publication were screened and included as grey literature. The impacts assessed in this study were based on a global scale.

4.3.2 Impact assessments

Different impact assessment tools have been developed to quantify the impacts of invasive species (Nentwig et al., 2016; Nkuna et al., 2018). For this study, we used the Generic impact scoring system (GISS) as it integrates both ecological and socio-economic impacts (Nentwig et al., 2016) and has proven to be useful in assessing the impacts of invasive plants globally including South Africa (e.g. Novoa et al., 2016). The GISS is divided into two main categories, environmental and socio-economic impacts each with six different mechanisms. The environmental impacts consist of impacts (1) on plants or vegetation, (2) on animals, (3) through competition, (4) through disease transmission, (5) through hybridisation and (6) on the ecosystem. The socio-economic include impacts on (1) agricultural production, (2) animal production, (3) forestry production, (4) human infrastructure (5) human health and (6) human social life. For each category the impact level ranges from 0 (no known impacts or data deficiency) – 5 (highest impact) and the scenarios are described to ensure consistency (details on Nentwig et al., 2016). For analyses, the overall impact scores (ecological and socio-economic) per species was used.

4.3.3 Data analyses

The differences between the overall scores for the socio-economic and environmental impacts were tested using a t-test. Post hoc tests (ANOVA and Turkey HSD) were used to further investigate the significant differences between the levels of mechanism. To test the correlation between the impact scores and the number of papers used for each species we used Kendall's rank correlation. All the data were analysed using R 3.4.4 (R Core Team, 2018).

4.4 Results

Assessed impacts for the 16 invasive plant species showed the highest environmental impacts than socio-economic impacts (Figure 4.1a). There was no significant difference between the overall environmental and socio-economic impacts (t.test: $P > 0.05$). Among the 16 invasive plant species, *Lantana camara* (impact magnitude = 46) followed by the *Ailanthus altissima* (tree of heaven) (impact magnitude = 32) had the highest overall impact scores (Table 4.1). Environmental impacts scores were higher for *L. camara* and *Cinnamomum camphora* than the other species (Table 4.1). The highest socio-economic impacts scores were recorded for *L. camara* and *A. altissima* (Figure 4.1b). Four plant species that had relatively no environmental impacts include *Psidium guajava*, *Cestrum laevigatum*, *Duranta erecta* and *Toxicodendron succedanea*. Two species that had no socio-economic impacts were *Ardisia crenata* and *Morus alba*. *Ailanthus altissima* scored the maximum impact on the socio-economic category through human social life (i.e. loss of recreational activities, tourist attraction, see Nentwig et al., 2016; Supplementary material Table S4.1). Some species showed low overall impact scores but scored higher (the maximum impact score of 5) in some mechanisms e.g. *M. alba* (impacts through hybridisation), *C. camphora* (impacts on plants or vegetation), *Rubus cuneifolius* (impacts on ecosystems) and *Schinus terebinthifolius* (impacts on plant or vegetation) (Figure 4.1b; Supplementary material Table S4.1). Most of the impacts recorded for the socio-economic category were through animal production, agricultural production and human health and the least impacts were on human infrastructure (Figure

Table 4.1. The sum of environmental and socio-economic impacts scored for 16 fruited invasive plant species. Species that scored a maximum impact score of 5 in any of the mechanisms are highlighted in bold. For the detailed impact assessment see supplementary material, Table S4.1).

Scientific names	Common names	GISS score				Region of origin
		NEM BA category	Environmental	Socio-economic	Total	
<i>Ailanthus altissima</i>	Tree of heaven	1b	13	19	32	Asia (China)
<i>Ardisia crenata</i>	Coral bush	1b	3	0	3	Asia
<i>Cestrum laevigatum</i>	Inkberry	1b	0	3	3	South America (Brazil)
<i>Cinnamomum camphor</i>	Camphor tree	1b	16	2	18	East Asia
<i>Duranta erecta</i>	Forget-me-not-tree	3	0	1	1	America
<i>Eugenia uniflora</i>	Surinam cherry	1a	2	2	4	South America (Brazil)
<i>Lantana camara</i>	Lantana	1b	23	19	42	Central and South America
<i>Melia azedarach</i>	Syringa	1b	3	2	5	Asia, Australia
<i>Morus alba</i>	White mulberry	2	8	0	8	Asia
<i>Psidium guajava</i>	Guava	2	0	6	6	America
<i>Rhus succedanea</i>	Wax tree	1	0	3	3	Asia
<i>Ricinus communis</i>	Castor-oil plant	1b	4	2	6	Africa
<i>Rubus cuneifolius</i>	American bramble	1b	10	4	14	North America
<i>Schinus terebinthifolius</i>	Brazilian pepper tree	1b	11	5	16	South America (Brazil)
<i>Solanum mauritianum</i>	Bugweed	1b	12	7	19	South America
<i>Syzygium jambos</i>	Rose apple	3	5	6	11	South - East Asia

2a; Supplementary material Table S4.1). Most environmental impacts were through impacts on plants or vegetation, ecosystem and animals and the least impacts were through hybridisation (Fig. 4.2b; Supplementary material Table S4.1). There were no significant differences between the mechanisms in both categories (socio-economic and environmental) (Turkey HSD: $P > 0.05$; Fig. 4.2). We found that 14 (86%) of the 16 plants species had no records of causing socio-economic impacts through impacting human life and environmental impacts through hybridisation. Most records of alien invasive plant species were mostly for the

environmental mechanisms than socio-economic mechanism. The total number of papers used for the impact assessment was 103 (see supplementary material Table S4.1 for a list of the data sources used) and there were significant differences between the number of papers and the scored impacts (Kendall's Tau: $\tau = -0.15$; $p < 0.05$).

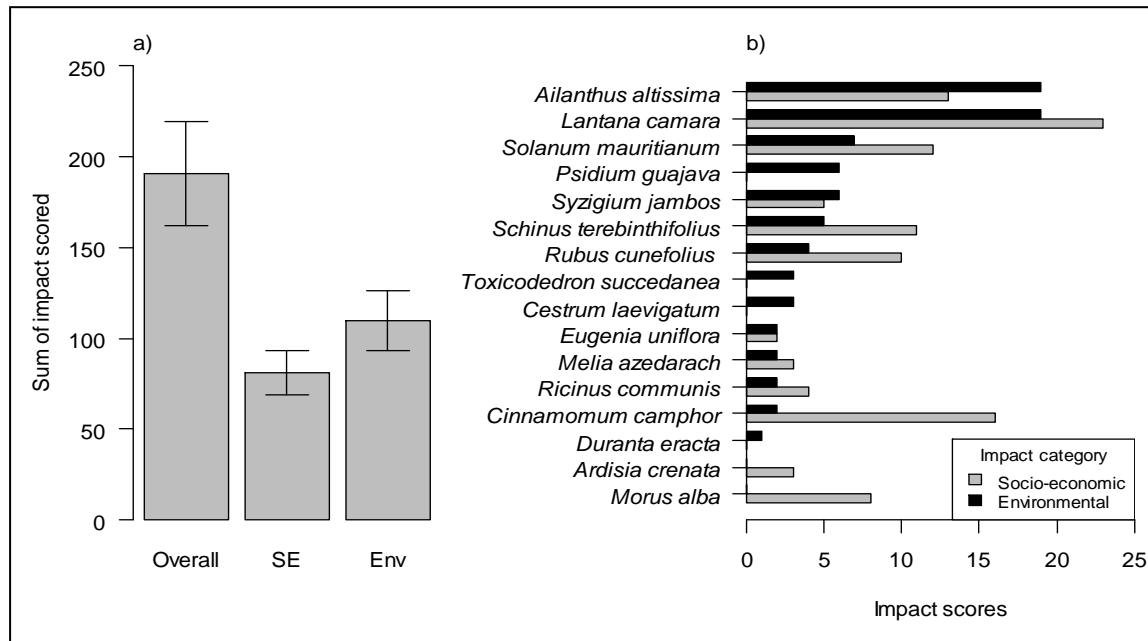


Fig. 4.1. The sum of (a) socio-economic and environmental impact magnitude and (b) impact scores for the socio-economic and environmental impact category for all the sixteen fleshy-fruited invasive plant species in South Africa in the present study (SE = socio-economic; Env = environmental).

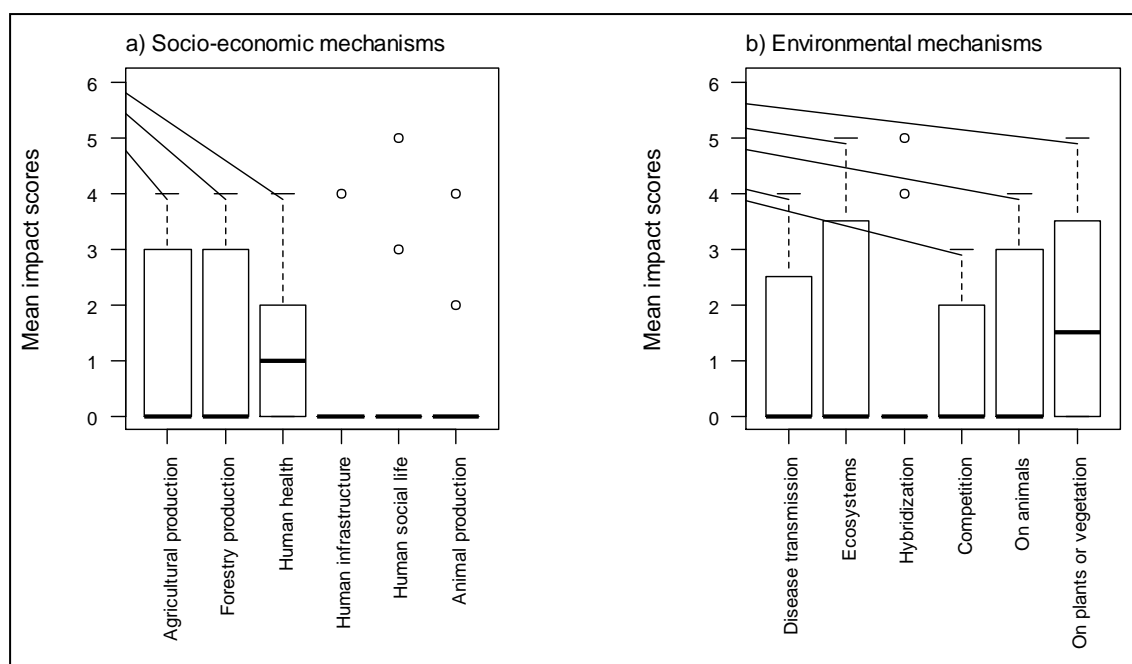


Fig. 4.2. The mean impact scores for (a) the socio-economic mechanisms and (b) for the environmental mechanisms in South Africa in the present study.

4.5 Discussion

This study is the first to assess environmental and socio-economic impacts using the GISS system focusing mainly on fleshy-fruited invasive plant species in South Africa. In the present study, global impacts assessment of 16 fleshy-fruited invasive species indicated that 12 species had environmental impacts and 14 had socio-economic impacts. The high proportion of species with environmental and socio-economic impacts could be attributed to the fact that the 16 selected species had already been listed in the NEMBA, indicating their high potency in invasiveness. This is in support of previous studies that have indicated that the introduction and establishment of alien species are associated with certain impacts (Pyšek and Richardson, 2010; Vilà et al., 2011; Sitzia et al., 2016; Rumlerová et al., 2016). The high potential invasiveness of fleshy fruited alien species has widely been attributed to avian dispersers, which can disperse the seeds over large distances (Jordaan & Downs, 2012;

Rejmánek, 2014). The dispersion of alien invasive fleshy-fruited species over long distances and large areas has a huge cost bearing on management and would require multi-pronged approaches. Two species with the highest overall impacts were *L. camara* (Lantana) and *A. altissima* (tree of heaven), indicating that they should be prioritised in the management of alien species. *L. camara* is profuse and relative resilient, making it dominant in both marginal and favourable conditions where other species would otherwise struggle. Interestingly *C. camphora* (camphor tree) had a higher environmental impact than *A. altissima* and this highlights the importance of considering both environmental and socio-economic impacts in risk assessment studies. The overall can be useful in broad recommendations but may negate the importance of specific species with specific impacts.

Environmental impacts associated with fleshy-fruited invasive plant species were mainly on ecosystems, plants or vegetation and some species had the highest impact scores on these mechanisms, for example, *R. cuneifolious* (American bramble), *S. terebinthifolius* (Brazilian pepper tree) and *C. camphora* (camphor tree). High environmental impact scores signify major threats to the environmental sector. These results corresponded to previous studies that have also shown similar findings on environmental impact mechanisms associated with invasive plant species (Vilà et al., 2011; Yazlik et al., 2018). Impacts on ecosystem functioning manifest in different ways including integrating into ecosystems networks (Voigt et al., 2011) changing pollination and seed dispersal networks that are important ecological processes. Changes in these two ecological functions (i.e. pollination, seed dispersal) result in the reduction of overall biodiversity (Fuster et al., 2019).

Impacts on human health, forestry and agricultural production were the main socio-economic impacts that were associated with fleshy-fruited invasive species in the present study and *L. camara* and *A. altissima* had the highest impacts. Similarly, a study in Turkey

showed that socio-economic impact mechanisms are through agriculture and human health (Yazlik et al., 2018). The major impacts on forestry production may be because of forests being identified as an important introduction pathway of many invasive tree and shrub species (Rejmánek 2014; Sitzia et al., 2016). Although some of these species are forest edge species it is important that they are included in forest management (Sitzia et al. 2016). Impacts on agriculture and human health were indirect and were through hosting pests that are potentially damaging to agricultural crops or pose a threat to human health. Also, invasive plants form thick stands that generally reduce the productivity of the land. It is important that management of invasive plants is not only targeting protected areas and should also be implemented in agricultural areas as impacts associated with invasive plants are both environmental and socio-economic (Yazlik et al., 2018). This is particularly important for sub-Saharan African countries with agriculture-dominated economies and livestock and crop farming constitute the largest agricultural sector (Pratt et al. 2017).

Fleshy-fruited invasive species were shown to have relatively few or generally lower impacts on human infrastructure, except for *A. altissima* (which scored the maximum impact. This is mainly because the impacts of alien plant species on human infrastructure (e.g roads, traffic infrastructure, see Nentwig et al., 2016) remain poorly explored. A total of six species in the present study showed either no environmental or socio-economic impacts. Similarly, a previous study in Europe that assessed the impacts of invasive two plant species using the GISS showed no environmental or socio-economic impacts (Rumlerová et al. 2016). This is a result of studies focusing on certain impacts or the selection of species with impacts that are already known (Pyšek et al., 2012; Rumlerová et al., 2016; Schirmel et al., 2016; White et al., 2019). Previous studies have noted the influence undocumented or lack of peer-reviewed information in quantitative impact assessment studies (McGeoch et al., 2012; Moshobane et al., 2019; Verbrugge et al., 2019).

For example, *P. guajava* has major ecological impacts in Zululand, KwaZulu-Natal, South Africa where this species has displaced native vegetation (C.T Downs). Consequently, the impacts on ecosystem or vegetation posed by this species are misrepresented in the present study. This highlights the importance of re-assessing impacts of species once data are available or published in the case of using assessment tools that use peer reviewed literature. Some species in the present study had low overall impact scores but scored the highest magnitude score for some mechanisms, for example, *M. alba* (white mulberry), *C. camphora* and *R. cuneifolius*. Similarly, a study that assessed the impacts of grasses using the GSSI showed similar results where two grass species with low overall impact had high magnitude scores for certain mechanisms (Nkuna et al., 2018). This is particularly interesting as it raises an important question that should species with high overall impact score be considered as high priority species or should species with low overall impact scores but high magnitude scores for certain mechanisms be of concern (Nkuna et al., 2018). Also, this is important as different sectors (i.e. health, forestry, agriculture) and stakeholders have different priorities and the risk perceptions of stakeholders are different (Hagen & Kumschick, 2018; White et al., 2019). For example, in practice, it is important that all mechanisms categories are assessed, and different sectors can make informed decisions if the introduction of species is likely to have impacts as the priorities of agriculturalists will be different to that of conservationists or the forestry industry.

In the present study, there were significant differences between the scored impacts and the number of papers used, well-studied plant species scored significantly higher impacts than species with less or no impacts studies. In general, the negative impacts of some species, especially those with economic value (i.e *P. guajava*, *R. communis*, *R. cuneifolius*), are often overlooked because of their beneficial uses. The research efforts of assessing the impacts of economic important

invasive plants are potentially complicated by the trade-off between economic importance and their damages resulting in misrepresentation of impacts. Indeed, Zengeya et al., (2017) assessed the impacts and benefits of invasive species and showed that management of *P. guajava* has resulted in stakeholder conflict in South Africa because of the economic and intrinsic value of the plant. As a result of research bias, impacts of species that have been extensively studied are bound to be higher than that of species less frequently investigated. Also, it has been reported that species with major economic impacts attract scientific attention and this improves understanding of their ecological impacts (Pyšek & Richardson, 2010). This may potentially explain the good publication record on the impacts associated with *L. camara* and *A. altissima*. Progress has been made in studying alien species impacts but there is still a publication bias as the impacts of some species remains unknown (Pyšek et al., 2012; Nentwig et al., 2016; Novoa et al., 2016; Rumlerová et al. 2016). It was not the aim of this study to assess the limitations of this tool, therefore, both scientists and decision-makers that aim to manage alien invasive species should consider both the benefits and costs of preventing the introduction of species with high impact scores or their management after introduction and establishment. This problem highlights the need for further studies to evaluate the socio-economic and ecological impacts posed by fleshy-fruited invasive plant species. Evaluating the social-related impacts of invasive species will increase different stakeholder engagement and scientific citizenship (Estevez et al., 2014; Crowley et al., 2017; Potgieter et al., 2019).

4.5.1 Conclusions

Assessing socio-economic and environmental impacts of fleshy-fruited invasive plant species in South Africa showed that these species pose both ecological and socio-economic impacts. This study also highlighted that the impacts of many fleshy-fruited invasive species

are not documented. We recommend management to prioritize species with high overall impact scores (*L. camara*, *A. altissima*, *C. camphora*) including species with low overall impact scores but high impact magnitude for certain mechanism (*M. alba*, *R. cuneifolius*, *S. terebinthifolius*) as the impacts are inevitable. The introduction pathways of these fleshy-fruited invasive plants species need to be identified and managed to prevent their future spread especially small, fleshy fruited ones attractive to native bird species are inevitably going to become part of the ecosystem. The results of the present study showed that different sectors are affected by invasive plant species and this emphasises the need for collaboration of different stakeholders in biological invasions management. In South Africa, not all local municipalities are capacitated to implement management strategies to effectively manage invasive species (McLean et al., 2018). Therefore, despite the different mandates for different departments or sectors in South Africa effective management of invasive plant species requires collaboration at a national and regional level including and adding a socio-economic dimension to the management strategies to ensure inclusivity and transparency. We recommend that more research is done to evaluate the impacts especially of socio-economic impacts associated with fleshy-fruited invasive plants species.

4.6 Acknowledgments

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4.7 References

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4.8 Supplementary information

Table S4.1 Environmental and socio-economic mechanism impact scores of fleshy-fruited invasive plant species assessed using the Generic Impact Score System (GISS).

Species	Common names	Environmental mechanisms							Socio-economic mechanisms							Overall scores	Number of literature
		Plants or vegetation	Animals	Competition	Diseases transmission	Hybridization	Ecosystems	Environmental total	Agricultural production	Animal production	Forestry production	Human Infrastructure	Human health	Human social life	Socio-economic total		
<i>Ailanthus altissima</i>	Tree of heaven	4	3	2	0	0	4	13	3	0	4	4	3	5	19	32	17
<i>Ardisia crenata</i>	Coral bush	3	0	0	0	0	0	3	0	0	0	0	0	0	0	3	1
<i>Cestrum laevigatum</i>	Inkberry	0	0	0	0	0	0	0	3	0	0	0	0	0	3	3	5
<i>Cinnamomum camphor</i>	Camphor tree	5	3	2	3	0	3	16	0	0	0	0	2	0	2	18	1
<i>Duranta erecta</i>	Forget-me-not-tree	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	7
<i>Eugenia uniflora</i>	Surinam cherry	0	0	0	2	0	0	2	2	0	0	0	0	0	2	4	1
<i>Lantana camara</i>	Lantana	4	4	3	4	4	4	23	4	4	4	0	4	3	19	42	25
<i>Melia azedarach</i>	Syringa	0	0	0	0	0	3	3	0	0	0	0	2	0	2	5	3
<i>Morus alba</i>	White mulberry	0	0	0	3	5	0	8	0	0	0	0	0	0	0	8	2
<i>Psidium guajava</i>	Guava	0	0	0	0	0	0	0	3	0	3	0	0	0	6	6	4
<i>Rhus succedanea</i>	Wax tree	0	0	0	0	0	0	0	0	0	0	0	3	0	3	3	2
<i>Ricinus communis</i>	Castor-oil plant	3	1	0	0	0	0	4	0	0	0	0	0	2	2	6	4
<i>Rubus cuneifolius</i>	American bramble	3	0	2	0	0	5	10	0	2	2	0	0	0	4	14	6
<i>Schinus terebinthifolius</i>	Brazilian pepper tree	5	3	0	0	0	3	11	0	0	2	0	3	0	5	16	10
<i>Solanum mauritianum</i>	Bugweed	3	3	0	2	0	4	12	3	0	3	0	1	0	7	19	8

Species	Common names	Environmental mechanisms							Socio-economic mechanisms							Overall scores	Number of literature
		Plants or vegetation	Animals	Competition	Diseases transmission	Hybridization	Ecosystems	Environmental total	Agricultural production	Animal production	Forestry production	Human Infrastructure	Human health	Human social life	Socio-economic total		
<i>Syzgium jambos</i>	Rose apple	0	0	2	3	0	0	5	3	0	3	0	0	0	6	11	6

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CHAPTER 5

Conclusions and recommendations

5.1 Introduction

Biological invasions are a component of global and are a major threat to biodiversity on a global scale (Davies et al., 2016). Fleshy-fruited invasive plant species are amongst the most damaging invasives worldwide (Thabethe et al., 2015). South Africa is under threat of the environmental, social and economic changes that are resulting from fleshy-fruited invasive plant species. The magnitude of impacts varies across different habitat types and species and frequently disturbed systems are more susceptible to invasions (Fontúrbel et al., 2017). Understating which species have major impacts is important for allocating limited resources and prioritising species for management. The mutualistic relationship with avian seed dispersers is key to their invasiveness potential and success (Aslan et al., 2011; Jordaan et al., 2011; Ramaswami et al., 2016). The successful interaction of avian-mediated seed dispersal is influenced by the bird and plant species traits (Carmona et al., 2016). Hence, the functional trait approach can be used to understand seed dispersal and invasion dynamics. This study aimed to assess avian-mediated seed dispersal, ecological and socio-economic impacts of fleshy-fruited invasive plant species. The objectives were to: (1) predict avian seed dispersers of fleshy-fruited invasive species; (2) determine the avian species dispersing the seed of *L. camara*; and (3) determine socio-economic and ecological impacts of fleshy-fruited invasive plant species.

5.2 Predicted avian dispersers of fleshy-fruited invasive species in a fragmented forest

Habitat fragmentation is a major biodiversity threat and facilitates the invasion of alien species in forest systems. Fleshy-fruited invasive species are amongst the worst invaders in the world and their invasiveness potential is increased by mutualistic relationships with seed dispersers.

The success of these mutualistic relationships is dependent on the functional traits of both plant and avian dispersers. Therefore, seed dispersal can be understood using a functional trait approach that provides a predictive ability to understand ecological processes. Avian seed dispersers of fleshy-fruited invasive plant species were predicted using functional traits that are important for avian-mediated seed dispersal to understand invasion dynamics in a fragmented forest (Chapter 2). The use of multivariate analyses showed that avian seed dispersers and fleshy-fruited invasive plant species differ in the functional traits that are important for seed dispersal. For fleshy-fruited plant variation was on the morphological traits (seed size, fruit size) and the phonological traits (fruiting length). For avian species the variation was on the morphology (body size, gape width, bill length), abundance and habitat specificity. We predicted that avian species that are potentially dispersing invasive plants in were forest generalist and abundant species persisting in the fragmented forest. Fleshy-fruited invasive plant species that were predicted to be effectively dispersed were small-seed, open habitat species with longer fruiting length including lantana, white mulberry, Brazilian pepper and bugweed. Future infestations were predicted to be along forest margins or gaps and these areas should be prioritised for management.

5.3 Potential avian seed dispersers of *Lantana camara*

Management of well-established fleshy-fruited invasive plant species requires an ecological understanding of processes underpinning successful spread (Ramaswami et al., 2016). In South Africa, there is limited information on the assemblage of native avian species feeding on a highly invasive plant *L. camara* (Ramaswami et al., 2016). Bird species potentially dispersing *L. camara* seeds were assessed using manual observations on shrubs with ripe fruits (Chapter 3). Avian species were shown to be primary seed dispersers of *L. camara* and the dark-capped bulbul was potential the main quantitative effective disperser (Chapter 3). The study showed

that species that are potentially contributing to the spread of *L. camara* in two sites in KwaZulu-Natal were generally relatively small generalist bird species. Potential seed dispersal distances predicted using the body mass of avian species showed that long seed dispersal distances are rarely limited by rare large frugivore species (Chapter 3). These interactions have conservation and management implications and highlight the importance of planting native fruiting species to provide an alternative food source.

5.4 Socio-economic and ecological impacts posed by fleshy-fruited invasive plant species

The impact of alien invasives vary and factors that influence the nature of the impact include the invasiveness of the species and the receiving environment (Zengeya et al., 2017). Effective management requires quantitative impact assessment tools that are comparable across different species and habitat types (Kumschick et al., 2017). In South Africa, a comprehensive unbiased categorisation of species is lacking, therefore knowledge, if alien invasive plant species with major impacts are being prioritised for management, is important to guide the allocation of funds to high priority species. Environmental and socio-economic impacts were assessed for 16 fleshy-fruited invasive plant species that are listed in the legislative instrument for alien species management in South Africa, the South African National Environmental Management; Biodiversity Act (NEMBA) (Chapter 4). The impacts were assessed using a generic impact scoring system that is based on scientific evidence. The findings of the study showed that species with high impacts were *L. camara*, *A. altissima* and *C. camphora* and need to be prioritised for management (Chapter 4). We found information gaps, especially for socio-economic mechanisms. Therefore, there is a need for studies that assess social-related impacts posed by alien invasive plant species. One finding from this study is that insufficient attention is being given to the potential ecological and socio-economic threats of those fleshy-fruited alien invasive plant species that are economically valuable. Further, different sectors will be

impacted differently to the threat posed as the impact of specific plants may be quite different for different sectors. This points to the need for greater communication *across sectors* in addressing alien invasive plant species. This has implications for the NEMBA listing and emphasises that species that are beneficial to one sector at the expense of other sectors need stakeholder engagement. When affected stakeholders engage directly prior to listing, the chances of an equitable management strategy to be reached is increased (Zengeya et al., 2017). Also, the results showed that

5.5 Final conclusions and recommendations

The aim of this study was to assess avian mediated seed dispersal, and the ecological and socio-economic impacts of fleshy-fruited invasive plant species. The results of the study showed the importance of ecological processes in the spread of alien invasive species. The interaction of avian species and fleshy-fruited invasive plants was shown to promote the invasiveness of the plants. The study highlighted the importance of these interactions in management and conservation. Also, the study revealed the importance of stakeholder engagement in the selection of species to be targeted for management. Further studies should determine the social dimension and human impacts of alien invasion to improve the research biases and the quantitative assessments. It is recommended that the removal of *L. camara* be made a priority by landowners and conservation managers to reduce the spread. A restoration approach that can be recommended to reduce colonisation is destroying the seed bank of the plant so that fewer seeds are viable and can germinate.

5.6 References

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