Effects of land-use changes on the distribution and use of *Ficus* species by frugivores in the urban mosaic landscape of Durban, KwaZulu-Natal, South Africa

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GENERAL ABSTRACT

Land-use change is one of the greatest threats to biodiversity. Over the years, these changes potentially reduced ecosystems capacity to sustain food production for vertebrates. *Ficus* (figs; Moraceae) is one of the largest plant genera in lowland tropical rainforests, with more than 850 described species distributed worldwide and 124 species in Africa. Fig trees occupy diverse habitats and attain a wide range of growth forms, including large woody climbers, hemi-epiphytes, trees, and shrubs. Over 1200 species globally feed on *Ficus* fruits and over 10% of the world's birds and 6% of mammals consume figs, making them the most widely consumed plant genus. Fig-fruiting phenology is such that they are generally available during periods of food scarcity and may influence entire faunal communities, particularly as a dry season staple food. Therefore, it is a well-known key fruit resource component in tropical forests and one of the most important genera sustaining numerous frugivores across different landscapes. In a mutually beneficial relationship, the plants also benefit from seed dispersal by frugivores taking seeds away from the parent plants to locations of fewer pathogens, enhancing germination and plant recruitment. This study was concerned with the interactions between fruit-producing plants and fruit-eating animals across an urban mosaic landscape in KwaZulu-Natal, South Africa. Specifically, the study focused on *Ficus* spp. of conservation importance and keystone species. Despite the critical role that figs play in many frugivores' ecology, there is relatively little information on the distribution and diversity of *Ficus* species along forest-urban gradients in relation to different land uses and frugivore foraging behaviours in the study area. Details of the relationships between different components of the frugivore-seed disperser and different fig species also remain unclear. Thus, this study enhances the understanding of the role of birds, bats and other mammals in seed dispersal, germination, and the effect of land-use changes on fig-frugivore interactions, which is critical for informing conservation and management strategies.

PREFACE

The data described in this thesis were collected in the urban-forest mosaic landscape of Durban, eThekwini Municipality, KwaZulu-Natal, South Africa, from May 2019 to January 2021. 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 Doctor of Philosophy 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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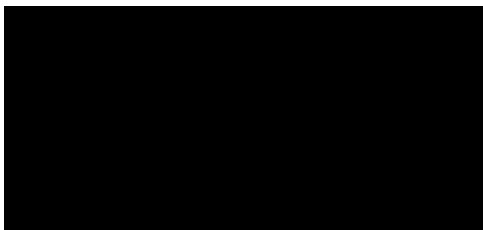…………………………..

Professor Colleen T. Downs

Supervisor

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DECLARATION 1 – PLAGIARISM

I, Islamiat Abidemi Raji, declare that

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DECLARATION 2 – PUBLICATIONS

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

Publication 1: Published in Acta Oecologica

Ficus-frugivore interactions, especially in areas of land-use change, in Africa: A systematic review

Islamiat Abidemi Raji & Colleen T Downs

Author contributions: IAR conceived paper with CTD. CTD sort funding. IAR collected and analysed data and wrote the paper. CTD contributed valuable comments to the manuscript.

Publication 2: In review -Journal of Ornithology

The role of avian frugivores in the germination of seeds of fleshy-fruited *Ficus* species in KwaZulu-Natal, South Africa

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Author contributions: IAR conceived paper with VT and CTD. CTD sort funding. IAR collected and analysed data and wrote the paper. VT and CTD contributed valuable comments to the manuscript.

Publication 3: In review - Austral Ecology

Does *Ficus* species seed ingestion by Wahlberg's epauletted fruit bats enhance germination and seedling emergence?

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Publication 4: Provisionally accepted -African Journal of Ecology

Fruiting phenology, diversity and distribution of native *Ficus* species in an urban-forest mosaic landscape in KwaZulu-Natal, South Africa
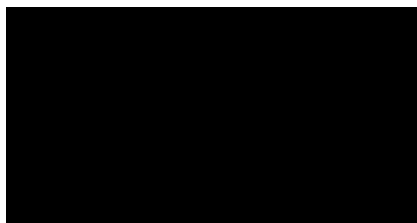
Islamiat Abidemi Raji & Colleen T. Downs

Author contributions: IAR conceived paper with CTD. CTD sort funding. IAR collected and analysed data and wrote the paper. CTD contributed valuable comments to the manuscript.

Publication 5: Formatted for -Acta Oecologica

Tree visitation and potential seed dispersal of keystone *Ficus* species by vertebrates in an urban mosaic landscape in eastern South Africa

Islamiat Abidemi Raji & Colleen T. Downs

Author contributions: IAR conceived paper with CTD. CTD sort funding. IAR collected and analysed data and wrote the paper. CTD contributed valuable comments to the manuscript.

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August 2021

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CHAPTER 1

General Introduction

1.1 Background

Anthropogenic land-use changes have severely fragmented indigenous forest habitats, thus affecting biodiversity across Africa, especially southern Africa (Lawes et al., 2007; Chibesa et al., 2017; Ehlers-Smith et al., 2017). Decreasing forest fragments could, directly and indirectly, impact species persistence by lowering local population sizes and increasing edge effects as the relative amount of edge habitat is greater in smaller fragments (Haddad et al., 2015; Mullu, 2016; Zambrano et al., 2020). In addition, this change leads to increased forest isolation that undermines the quality of forest habitats (Saunders et al., 1991, Wunderle 1997, Fischer & Lindenmayer 2007; Zambrano et al., 2020). It also adversely impacts the population of trees and a key ecological process such as seed dispersal, altering the pivotal role of seed dispersers in the regeneration and restoration of plant communities across forest ecosystems globally (Saunders et al., 1991, Wunderle 1997, Fischer & Lindenmayer 2007).

These land-use changes have been reported to result in the decline and loss of key dispersers in response to the loss of fruiting trees and alter the interaction structure of mutualistic networks (Cordeiro & Howe 2003, Kirika et al., 2008). Hitherto, it is known that species respond differently to change in land use because of different sensitivities to disturbances (Watson et al., 2005, Van Houtan et al., 2007). While some species may take advantage of habitat modification such as urbanisation, farmland or scattered trees within farmland, others may not. For instance, several studies (Rodriguez-Cabal et al., 2007; Kirika et al., 2008; Cordeiro et al., 2009; Lehouck et al., 2009; Uriarte et al., 2011; Fahrig, 2017) showed reduced frugivore numbers, fruit removal and seed dispersal of a *Ficus* tree species because of anthropogenic land-use changes resulting in the isolated and low population of this species. These results suggest that mutualistic interactions of keystone species can be

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susceptible to human forest disturbance with potential long-term effects on the biodiversity of tropical forests. Consequently, this loss of frugivores can lead to lower rates of seed dispersal (Cordeiro & Howe, 2003).

Ficus (figs; Moraceae) is one of the largest plant genera in lowland tropical rainforest, with more than 850 described species distributed worldwide (Frodin, 2004; Harrison, 2005; Chaudhary et al., 2012; Mabberley, 2017; Mohapatra et al., 2020), and about 124 species in Africa (Berg & Wiebes, 1992; Burrows & Burrows, 2003; Van Noort & Rasplus, 2020). *Ficus* is a woody plant genus that exhibits a vast diversity of ecologies, including different plant life-forms, a considerable range in morphologies including plant size/height and leaf size, and a broad spectrum of fruit types (Harrison et al., 2012). Globally over 1200 species feed on *Ficus* (Cottee-Jones et al., 2016; Corlett, 2017), and over 10% of the World's birds and 6% of mammal species consume *Ficus* fruit, making them the most widely consumed plant genus.

Figs (*Ficus*) play a prominent role in ecosystems. Their presence or absence could affect the occurrence of other species. Hence, figs are regarded as a keystone species (Bleher et al., 2003; Eshiamwata et al., 2006; Jeevanandam & Corlett, 2013; Walther et al., 2018; Mackay et al., 2018). Furthermore, figs have also been identified as an effective pioneer species because of their disproportionately large influence over their ecosystem in relation to both their abundance and biomass (Eshiamwata et al., 2006; Jeevanandam & Corlett, 2013; Walther et al., 2018). Fig-fruiting phenology is aseasonal resulting in low inter-annual variation in fruit production (Bianchini et al., 2015). Consequently, their fruits are typically available during seasons of food scarcity and may influence entire faunal communities, particularly as a dry season staple for birds, fruit bats and other mammals (Jeevanandam & Corlett, 2013; Makau, 2016). *Ficus* species have a great ability to attract frugivores across disturbed habitats as a result of their unique fruiting attributes, thus, proving to be a more effective restoration nucleus than other species (Cottee-Jones et al., 2016). However, the mutualistic interactions of keystone

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Ficus spp. may be sensitive to changes in land use (such as anthropogenic forest disturbance, deforestation and fragmentation) with potential long-term effects on the biodiversity along urban mosaic landscape.

1.2 Problem statement

Despite the critical role that figs play in the ecology of many frugivores, there is relatively little information on the distribution and diversity of *Ficus* species along urban-forest gradients in relation to their different frugivore use and interactions. Therefore, it is important to understand the effects of land-use changes on the frugivore-fig relationship as they play a critical role in ecosystem functions.

This research focuses on a single diverse plant genus of conservation importance, the fig plants (*Ficus* spp; Moraceae). We examined the distribution of *Ficus* species in the urban mosaic landscape of Durban, eThekwini Municipality, KwaZulu-Natal Province, South Africa, monitored their fruiting phenology and the interactions with fruit-eating animals.

1.3 Aims and objectives

This study aimed to map the distribution of keystone *Ficus* species in the urban mosaic landscape of Durban, eThekwini Municipality, KwaZulu-Natal Province, South Africa, and investigate their interactions with frugivorous animals. Therefore, the study examined the effect of gut ingestion by frugivores on germination success of *Ficus* species, monitored the fruiting phenology of *Ficus* species and frugivore visitors in the urban mosaic landscape. To achieve these aims, the following objectives were established:

- Determine the role of ingestion and gut passage by frugivores (fruit bat and birds) on the germination success and seedling emergence of fleshy-fruited *Ficus* species in KwaZulu-Natal, South Africa,

- Investigate the foraging behaviour of avian frugivores in relation to the dispersal of figs across different land-uses, and

- Determine the presence, abundance and diversity of *Ficus* species across different land uses along urban-forest gradients in the urban mosaic landscape of Durban, Ethikwini Municipality, KwaZulu-Natal.

1.4 Structure of the thesis

This thesis comprises of seven chapters; a brief introduction (Chapter 1, includes aims and justification), a review of the relevant literature (Chapter 2), followed by four data chapters then a final chapter with conclusions and management recommendations. All data chapters were formatted for submission to international peer-reviewed journals. Therefore, some repetition was unavoidable. The hypotheses or predictions, and outcomes are presented in the respective chapters.

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CHAPTER 2

***Ficus*-frugivore interactions, especially in areas of land-use change, in Africa: A**

systematic review

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Running header: Effects of land-use changes on fig-frugivore interactions in Africa

2.1 Abstract

Land-use change is one of the greatest threats to biodiversity. It is predicted that conversion of land and habitats will increase rapidly over the next few decades in Africa. Over the years, these changes potentially reduced the capacity of ecosystems to sustain food production for vertebrates. *Ficus* species (Moraceae), commonly known as figs, occupy diverse habitats and typically produce large numbers of nutritional fleshy fruits that are important to frugivores. However, a decline in *Ficus* spp. distribution because of land-use changes may negatively affect frugivores and their ecosystems (e.g. via seed dispersal). We systematically searched for studies on the distribution of *Ficus* spp. in Africa and their frugivore interactions together with the effects of land-use changes up until 2021. Our search resulted in 70 eligible papers. A total of 124 *Ficus* spp. were recorded across 30 African countries representing approximately 56% of the African countries. Cameroon had the highest record of 63 species, while Benin, Burundi, Ghana, and Rwanda had two, the least number of *Ficus* spp. recorded. East Africa had the highest *Ficus* spp. richness recorded (96 species), followed by southern Africa (74 species), Central and Northern Africa (72 species), and West Africa with the least (31 species) recorded. Information about the effect exerted by anthropogenic land-use changes on *Ficus*-frugivore interaction in Africa was limited. However, research has been conducted on the impact of anthropogenic land-use changes on plant-frugivore and frugivore feeding ecology. *Ficus* spp. fruit were identified as significant in the diets of various frugivores across Africa, as it is found globally. However, it is essential to understand the impacts of anthropogenic land-use changes on the mutual interaction between frugivores and *Ficus* spp. and the attendant consequences for ecosystem service provision.

Keywords: Figs, Frugivores, Africa, Urban-Forest gradients

2.2 Introduction

Land-use change is accelerating with increased human populations (Brown et al., 2014; Maseko et al., 2019; Herrmann et al., 2020). Land-use change is the greatest threat to biodiversity currently (de Lima et al., 2013; Ehlers Smith et al., 2017; Mahiga et al., 2019; Zungu et al., 2019). The rapid increase in land-use change and activities, especially involving forest conversion, has disproportionally led to species population declines (Farwig et al., 2008; de Lima et al., 2013; Chibesa and Downs, 2017; Newbold et al., 2020). This has resulted in widespread losses of tropical biodiversity and alteration of spaces where species grow and interact (Sekercioglu, 2002; Gibson et al., 2015; Lewis et al., 2015; Werema and Howell, 2016; Waston et al., 2018). Anthropogenic disturbances and land-use changes have forced some avian frugivores to permanently migrate to other areas (Maitima et al., 2009; Tilman et al., 2017; Newbold et al., 2020). Frugivores are more sensitive to direct human pressures than any other avian feeding guilds (de Lima et al., 2013; Rocha et al., 2015; Mahiga et al., 2019). Several studies in Africa have shown that frugivore abundance and seed dispersal decrease with increased land-use changes (Farwig et al., 2008; Kirika et al., 2008; Chibesa and Downs, 2017). Therefore, with increased land-use intensity, frugivore abundance and seed dispersal are negatively affected (Laube et al., 2008; de Lima et al., 2013; Schor et al., 2015). Since most frugivore species feed on *Ficus* spp. fruits in Africa, it is essential to understand the pattern of habitat use for effective management and conservation of *Ficus* spp. to enhance plant-frugivore interactions (Cordeiro et al., 2009; Chama et al., 2013).

A variety of habitat characteristics, like breeding space and nesting sites crucial for frugivore survival, are also lost with anthropogenic land modification (Gibson et al., 2015; Lewis et al., 2015; Waston et al., 2018; Zungu et al., 2019). Frugivores may decline or increase under different land-use regimes (Kirika et al., 2008), and there is still an insufficient

understanding of these patterns. As these changes have various effects on frugivores' interactions with plants, we focussed on *Ficus* spp. as our study species in this review.

Several criteria are used to define keystone plant species for frugivores; these include the ability to produce fruits during periods of scarcity, abundance in crop yield, and or the population size of animals that used the specific resources (White, 1994; Bleher et al., 2003; Herre et al., 2008). Figs (*Ficus* spp., Moraceae) are considered keystone species and are a diverse and ecologically significant component, especially of African flora (Berg and Wiebes, 1992; Shanahan et al., 2001; Burrows and Burrows, 2003). *Ficus* spp. fruit attract a diverse community of frugivores and provide a reliable diet for frugivore survival (Shananhan et al., 2001; Ronsted and Savolainen, 2007; Foster, 2014). The capacity to produce large nutritional fruits all year round, especially in the scarcity of other fruit resources, makes *Ficus* the most widely consumed plant genus (Shanahan et al., 2001; Bleher et al., 2003; Lomascolo et al., 2010; Daru et al., 2015). Examining fig-frugivore interactions across land-use changes can better understand the long-term effects of anthropogenic impacts on the interactions (Bascompte and Jordano, 2007).

In this review, we predicted that land-use changes would affect *Ficus*-frugivore interactions. These interactions are important in maintaining the ecosystems in which they exist. We, therefore, aimed to determine how *Ficus* spp. distribution and interactions with vertebrate frugivores may be affected by land-use change, especially along forest-urban land-use gradients in Africa. Consequently, we hoped to improve the current understanding of these issues by bringing together information from published studies and identifying possible gaps requiring further research. We achieved this by reviewing the literature on the effects of land-use changes on *Ficus* spp. distribution and their interactions with frugivorous vertebrates, especially birds and mammals.

2.3 Methods

2.3.1 Literature search strategy

Following the PRISMA guidelines (Moher et al., 2009; O'Dea et al., 2021), we conducted a systematic literature review. According to Roberts et al. (2007) systematic reviews have an advantage over other reviews in that they are methodologically repeatable. We obtained relevant peer-reviewed articles using the Thomson Reuters' Web of Science database (https://apps.webofknowledge.com), Google Scholar (https://scholar.google.co.za/), and Wiley Online Library (https://onlinelibrary.wiley.com/). Our search terms include publications on *Ficus*-frugivores interaction in Africa, land use effect on *Ficus* spp., and frugivores. We used the following keywords and phrases, "*Ficus*" "*Fig trees,*" "*seed dispersal,*" "*seed dispersers,*" "*Frugivore,*" "*human modified-landscape,*" "*Land-use changes,*" "*land-use gradient,*" "*urban-forest gradient*" with Africa region specified in the search (Fig. 2.1, Supplementary Fig. S2.1). We further examined the bibliographies of relevant articles to ensure a comprehensive review of the literature. In addition, we searched Figweb for the distribution of *Ficus* spp. in Africa.

2.3.2 Data collection

We recorded the numbers of articles returned from each database and stored all the citations. We then filtered the articles from the different search engines and eliminated duplicated documents from our collated list (Fig. 2.1, Supplementary Fig. S2.1, Supplementary Table S2.1). We also reviewed the bibliographies of relevant articles. For an article to be included as relevant, it had to investigate fig-frugivore interaction, distribution, or phylogeny of figs or its effect as a keystone species or/and effect of land-use changes on figs and frugivore. For the retained papers, we recorded the location of the study. As database searches may miss potentially relevant works, additional searches were conducted to uncover other potentially

eligible published works. We used the reference sections of peer-reviewed published articles to determine: (1) potentially relevant articles and (2) journals that contained several relevant studies. Potentially relevant articles were then manually searched using the Google Scholar search engine. Although systematic reviews aim to be as comprehensive and representative of the literature as possible, publication bias can still occur when authors do not submit their publication results (Lipsey and Wilson, 2001; Borenstein et al., 2011).
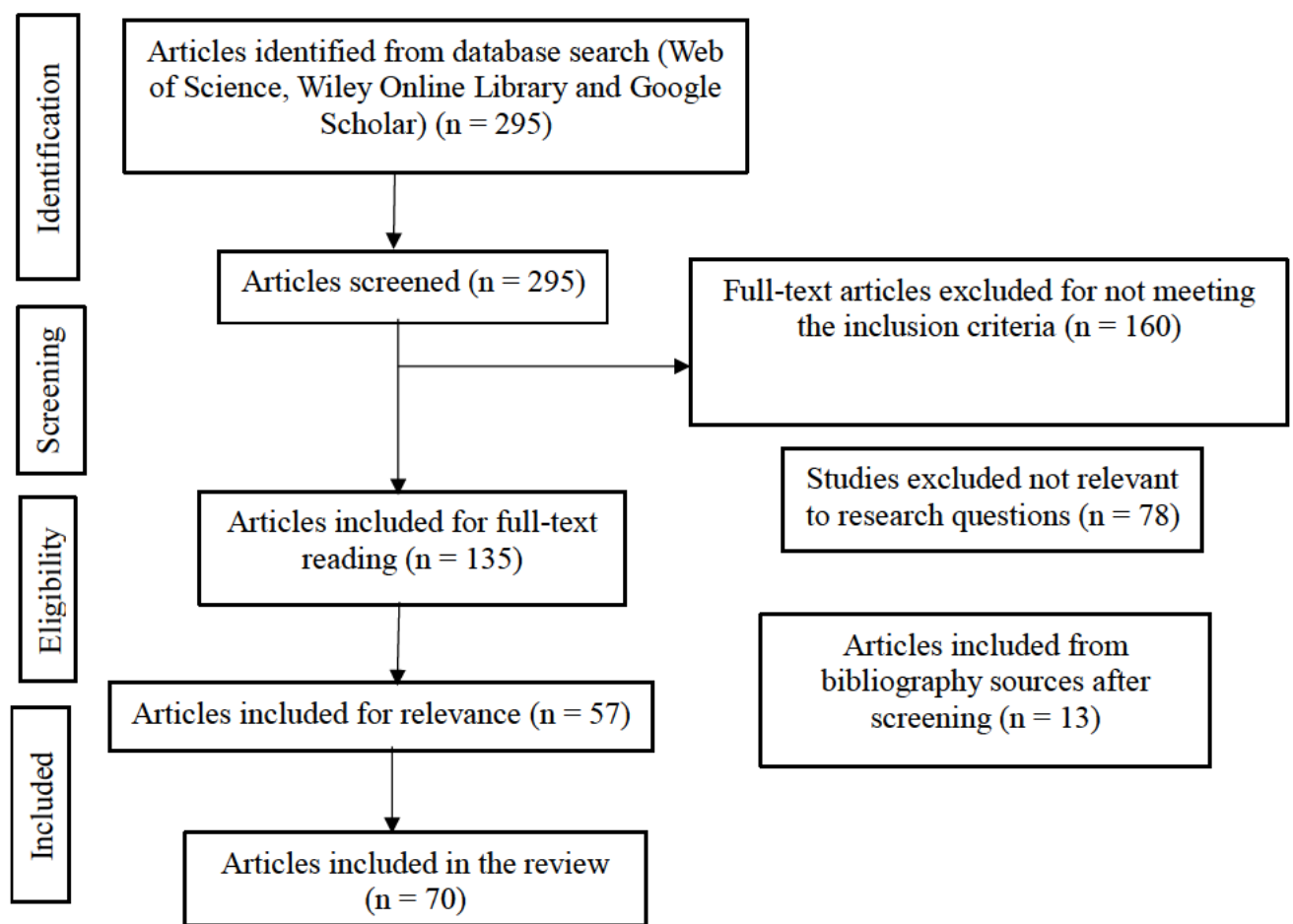
Fig. 2.1. Flow chart based on PRISMA protocols (O'Dea et al., 2021) illustrating how papers were selected or discarded

2.4 Results and Discussion

We identified 295 relevant peer-reviewed papers for potential inclusion. Each article's abstract and title were checked. We excluded articles that did not meet the inclusion criteria because they were not relevant to fig-frugivores, and research was not conducted in Africa. References from the Figweb were also added, and the bibliographies of relevant articles were also searched for additional references. The full text was read for the remaining articles, and 70 of these met the inclusion criteria and were included in our review (Fig. 2.1, Supplementary Fig. S2.1, Supplementary Table S2.1).

2.4.1 Fig distribution in Africa

In total, 124 species from the genus of *Ficus,* comprising ten subsections, five sections, and five subgenera, were recorded in 30 African countries (~56% of African countries) (Fig. 2.2-2.3, Supplementary Tables S2.2-2.7, Supplementary Fig. S2.2). Data were gathered from the Figweb (http://www.figweb.org/*Ficus*/index.htm) with the country name specified (e.g., South Africa *Ficus*: Figweb), and complemented with supporting literature (Berg and Wiebes, 1992; Burrows and Burrows, 2003; Van Noort and Rasplus, 2020). Most records were from Cameroon with 63 *Ficus* spp., while Benin, Burundi, Ghana, and Rwanda had the least with two *Ficus* spp. each (Fig. 2.2, Supplementary Fig. S2.2). East Africa has the highest *Ficus* spp. richness (96 species), southern Africa (74 species), Central and Northern Africa (72 species), and West Africa with the least species richness recorded (31 species) (Supplementary Tables S2.2-2.7, Fig. 2.3). *Ficus sur* and *F. ingens* were the most recorded with 20 countries out of the 30 Africa countries listed in this study (Supplementary Tables S2.2-2.7, Fig. 2.3).
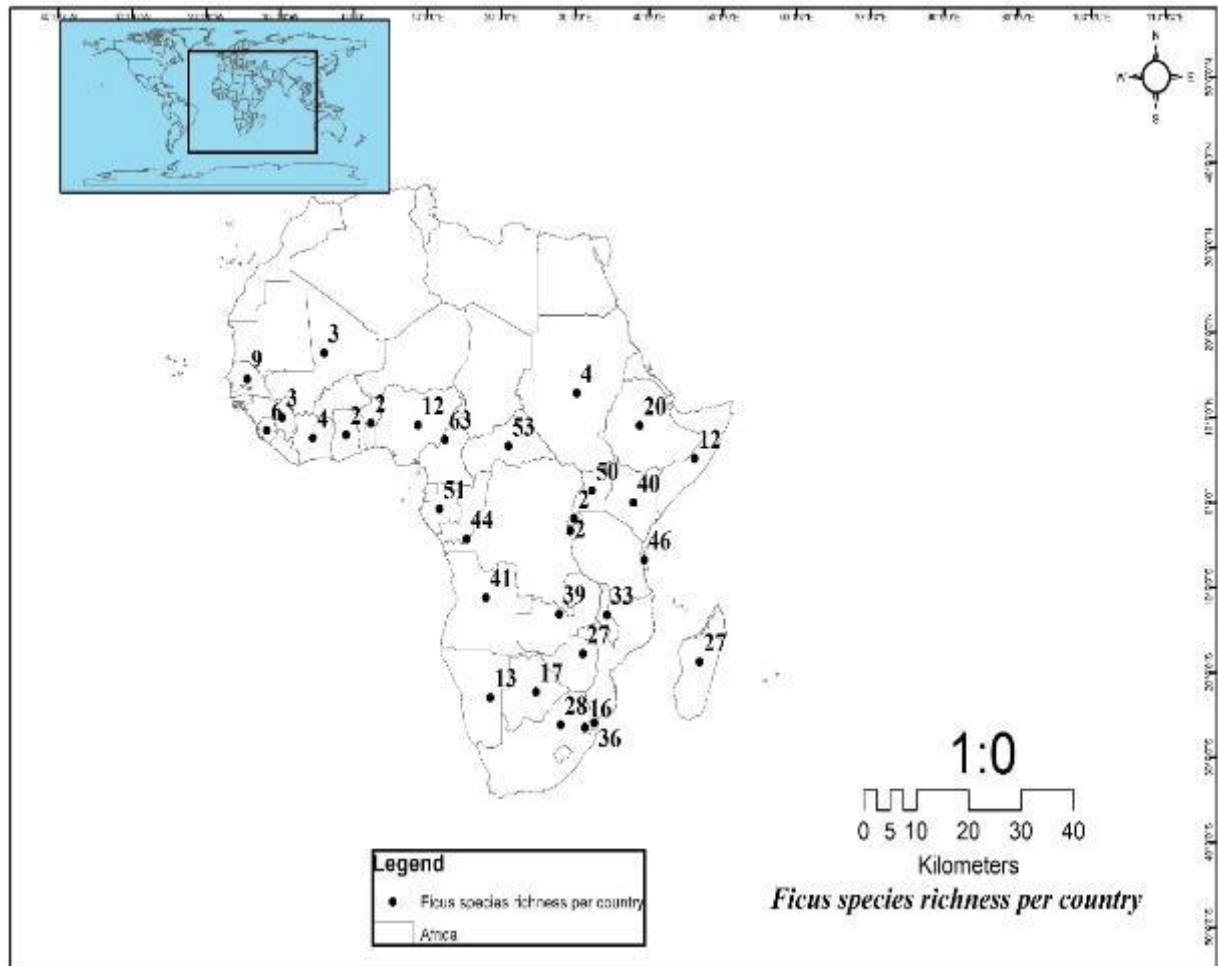
Fig. 2.2. *Ficus* spp. richness per country in the present study (Berg et al., 1989; Berg and Wiebes, 1992; Lipsey and Wilson, 2001; Burrows and Burrows, 2003; Luke, 2005; Daru et al., 2014; Van Noort and Rasplus, 2020)

Ficus spp. trees occupied diverse habitats ranging from rainforests, under canopies, rivers and cliffs, and human-modified landscapes (Burrows and Burrows, 2003). They may also attain a wide range of growth forms such as large woody climbers, hemi-epiphytes, trees, and shrubs (Serrato et al., 2004; Ipulet, 2007; McLeish et al., 2010; Van Noort and Rasplus, 2020). *Ficus* spp. are suitable pioneer species and play a prominent role in the ecosystem, some of which could collapse if they were absent (Tweheyo and Obua, 2001; Tweheyo and Lye,

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2003). *Ficus* spp. distribution was reflected in the variety of animals recorded feeding on them across the different habitats, as shown from Figweb (http://www.figweb.org/*Ficus*/index.htm).

2.4.2 Fig-frugivore interactions

Ficus spp. trees are consistently identified as critically important components of tropical ecosystems (McGrew et al., 1988; Tweheyo and Obua, 2001; Tweheyo, 2003; Seltzer et al., 2013; Bortolamiol et al., 2014; Kagoro-Rugunda and Hashimoto, 2015). They are considered reliable food resources because they generally have relatively short intervals between fruiting events (Berg et al., 1989; Shananhan et al., 2001; Ronsted and Savolainen, 2007; Foster, 2014). The high dependency of frugivores on *Ficus* spp. results from their regular supply of fruit, with individual trees, repeatedly fruiting within a year (Shananhan et al., 2001; Foster, 2014). These are important attributes in the interactions between *Ficus* spp. and frugivores species (Tweheyo and Obua, 2001; Tweheyo and Lye, 2003; Adams and Snode, 2013; Seltzer et al., 2013; Kagoro-Rugunda and Hashimoto, 2015). Another *Ficus* spp. fruit attribute that enhances their attractiveness to vertebrate frugivores is that they are relatively easy to handle and consume (Tweheyo and Obua, 2003; Eshiamwata et al., 2006). *Ficus* spp. fruit have soft exocarps when ripe with small seeds that frugivores can easily eat while still attached to the stem. These attributes, combined with the typical *Ficus* spp. abundance in crop yield has led some researchers in Asia to describe them as the "fast food of the forest" (Lenz et al., 2015)

Ficus spp. trees' aseasonal fruiting patterns and fruit nutritional composition are further attributes that may enhance their attractiveness to vertebrate frugivores (Shanahan et al., 2001; Acipa et al., 2013; Compton and Greef, 2020). Comparative studies that analysed the nutrient content of *Ficus* spp. fruit and other tropical fruits in Uganda (Acipa et al., 2013) and South Africa (Wilson and Downs, 2012) found *Ficus* fruits to be 3.2 times on average higher in calcium and phosphorous than other studied tropical fruits. Therefore, figs are important in

avian and mammalian diets as calcium level is believed to be important for bone growth in many frugivores and eggshell development in birds (Shanahan et al., 2001; Wilson and Downs, 2012; Compton and Greef, 2020). However, *Ficus* spp. fruits have been noted to contain relatively low protein, carbohydrate, and lipid content than other tropical fruits (McLennan, 2013). Although different *Ficus* spp. show considerable variation in nutritional properties, *Ficus* spp. fruit can contain high levels of amino acids, potassium, magnesium, and sodium (Wilson and Downs, 2012; McLennan, 2013).

Numerous species of birds and mammals have been recorded visiting *Ficus* spp. in Africa's different landscapes (Table 2.1, Supplementary Table S2.8, Fig. 2.3). These range from West Africa (Daru et al., 2014) to southern Africa (Basabose, 2002; Bleher et al., 2003; Hart et al., 2013; Bonaccorso et al., 2014; Chibesa and Downs 2017), Central Africa (Kagoro-Rugunda and Hashimoto, 2015), and Eastern Africa (McGrew et al., 1988; Tweheyo and Obua, 2001; Tweheyo and Lye, 2003; Seltzer et al., 2013; Bortolamiol et al., 2014). Most *Ficus*-frugivore interactions recorded in this review were mostly in forest ecosystems (especially protected areas, National Parks and nature reserves, Table 2.2). However, isolated *Ficus* spp. trees were also recorded to persist in human-modified landscapes and interact with vertebrate frugivores there (Berg, 1989; Burrows and Burrows, 2003; Eshiamwata et al., 2006; Table 2.1).

2.4.2.1 Figs and chimpanzees

Chimpanzees (*Pan troglodytes*) are primarily frugivores; they feed mainly on ripe fruits (Sugiyama and Koman, 1979, 1992; Tweheyo and Obua, 2001; Tweheyo and Lye, 2003). Several researchers have reported *Ficus* spp. fruit as important in chimpanzees diets in various habitats across Africa (Table 2.1), ranging from West Africa savanna-dominated areas (Goodall, 1968; Sugiyama and Koman, 1979; Sugiyama and Koman, 1992) to East Africa woodland forest (Conklin and Wrangham, 1994; Newton-Fisher, 1999; Tweheyo and Obua,

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2001; Tweheyo and Lye, 2003), Central and Southern Africa (Tutin and Fernandez, 1993; Gross-Camp et al., 2009; Kagoro-Rugunda and Hashimoto, 2015). Over 70% *Ficus* spp. seeds were frequently identified in chimpanzee faeces each month, during periods of both high fruit availability and fruit scarcity (Kagoro-Rugunda and Hashimoto, 2015). *Ficus* spp. seeds have also been identified in 92% of chimpanzee faeces (n = 7,212) in the Democratic Republic of Congo by Basabose et al. (2002) and McLennan (2013) identified 87% *Ficus* spp. seeds in chimpanzee faeces in forest fragments amid agricultural lands of Bulndi, Uganda. However, some researchers termed *Ficus* spp. fruits as a fallback food have been reported as less preferred fruits than non-figs and were observed to be eaten by chimpanzees when non-figs were in short supply (Tutin and Fernandez, 1993; McLennan, 2013; Kagoro-Rugunda and Hashimoto, 2015). Several studies have shown that chimpanzees and other frugivores eat *Ficus* spp. fruit during periods of both scarcity and abundance of pulp fruits, regardless of the time of year. Therefore, *Ficus* spp. fruits are generally not fallback food; instead, they are daily keystone fruit foods (Tweheyo and Obu, 2001; Basabose, 2002; Tweheyo and Lye, 2003; Seltzer et al., 2013).

2.4.2.2 Figs and fruit bats

Several species of fruit-bat (Megachiroptera, Pteropodidae) have been recorded feeding on *Ficus* spp. fruit in East and southern Africa (Rollinson et al., 2013; Seltzer et al., 2013; Bonaccorso et al., 2014). They act as an effective seed dispersals agent for *Ficus* spp., among other mammals (Bonaccorso et al., 2014). Seed dispersal is critical for maintaining plant communities and ecosystem structure (Adams and Snode, 2013; Bortolamiol et al., 2014). The epauletted fruit bats (*Epomophorus wahlbergi* and *E. crypturus*) feed on large quantities of ripe figs that pass through their gastrointestinal tracts without damage and transport such seeds large distances (Shanahan et al., 2001; Bonaccorso et al., 2014). Adams and Snode (2013) and

Bonaccorso et al. (2014) recorded about 88-100% germination success of fig seeds passing the gastrointestinal tracts in their studies. Shanahan et al. (2001) recorded *Ficus* spp. fruit in the diet of at least 47 species of bats across 20 genera, over 88% of *Hypsignathus monstrosus* oral and faecal samples in Gabon, West Africa, contained *Ficus* spp. seeds (Gautier-Hion & Michaloud, 1989), and radio-tagged fruit bats in South Africa displayed movement patterns that largely reflected the distribution of ripe *F. sycomorus* in Kruger National Park, suggesting some degree of dietary reliance on *Ficus* spp. fruit (Bonaccorso et al., 2014).

2.4.2.3 Figs and bird species

Bird species such as hornbills (*Tockus* and *Bycanistes* spp.), turacos (*Tauraco* and *Corythaeola* spp.), pigeons (*Treron* spp.), parrots (*Poicephalus* spp.), lovebirds (*Agapornis* spp.), barbets (*Tricholaema* and *Trachyphonus* spp.), mousebirds (*Colius* and *Urocolius* spp.), orioles (*Oriolus* spp.), starlings (*Cinnyricinclus* spp.), bulbuls (*Pycnonotus* spp.), greenbuls (*Andropadus* and *Phyllastrepus* spp.) and thrushes (*Turdus* spp.), in southern Africa (Bleher et al., 2003; Kemp, 2005; Hart and Downs, 2013; Chibesa and Downs, 2017), East Africa (Kirika et al., 2008) and West Africa (Daru et al., 2015) have been recorded feeding on *Ficus* spp. fruit (Table 2.1, Fig. 2.3, Supplementary Fig. S2.2, Supplementary Table S2.8). Also, fallen fruits are eaten by francolins and several species of ground-dwelling doves (*Streptopelia* spp). Bleher et al. (2003) and Chibesa and Downs (2017), in their findings, recorded *Ficus* spp. fruit to be one of the preferred food items in the diets of Trumpeter Hornbills (*Bycanistes buccinator*) and several other bird species.

2.4.2.4 Figs and other mammals

Monkeys (*Cercopithecus* spp.), tree hyrax (*Dendrohyrax arboreus*), squirrel species (*Sciuridae* spp.), bushbabies (Galagidae), genets (*Genetta genetta*), African civet (*Civettictis civetta*), species of mongoose (Herpestidae) and humans have been recorded feeding on *Ficus* spp. fruit in East and southern Africa (Wrangham et al., 1996; Tweheyo and Obua, 2001; Beentje and Mbago, 2007; Adams and Snode, 2013, Table 2.1). *Ficus* spp. trees with large crowns size in conjunction with fruit crops have been documented as important for bushbuck (*Tragelaphus scriptus*), duikers (Cephalophini), suni (*Neotragus moschatus*), bushpig (*Potamochoerus larvatus*), small rodents and chimpanzees not only as a diet but also for social interactions, in East Africa (Goodall, 1968; Tweheyo and Obua, 2001; Tweheyo and Lye, 2003; Beentje and Mbago, 2007) and West Africa (Sugiyama and Koman, 1979; McGrew et al., 1998) (Table 2.1).

Table 2.1 Frugivores recorded interacting with Ficus spp. in different parts of Africa and across different land-use types (Note: Nomenclature has been updated to follow Chibesa and Downs (2017).

Frugivores	Study locations	Land-use types	Source
Bird Species			
Hornbill species			
Ceratogymna atrata	Cameron	Forest reserve and low land Forest	(Wang and Smith, 2002; Whitney et al., 1998)

Bycanistes brevis	Malawi,	Forest	(Dowsett-Lemaire, 1988)
	Kenya	Forest	(Engel, 2000; Githiru et al., 2005)
Bycanistes buccinator	Malawi	Forest	(Dowsett-Lemaire, 1988)
	South Africa	Urban-Forest Mosaics	(Lenz et al., 2011; Chibesa and Downs, 2017)
		Coastal forest	(Bleher et al., 2003)
Bycanistes cylindricus	Cameron		(Poulsen et al., 2002; Wang and Smith, 2002; Whitney et al., 1998)
Bycanistes fistulator	Cameron	Forest Reserve	(Poulsen et al., 2002)
Ceratogymna atrata	Cameroon		(Whitney et al., 1998)
Bycanistes subcylindricus	Uganda		(Kalina, 1988)
	Kenya		(Flörchinger et al., 2010)
Tockus alboterminatus	Kenya		(Engel, 2000)
Tockus fasciatus	Ivory Coast		(Jensch and Ellenberg, 1999)
	Gabon		(Gautier-Hion et al., 1985)
Bycanistes fistulator	Gabon		(Gautier-Hion et al., 1985

Bycanistes albotibialis			
Ceratogymna atrata			
Bycanistes brevis	Tanzania	Nature reserve	(Cordeiro et al., 2016)
Schalow's turaco *(Tauraco schalowi)*	Malawi	Forest/Woodland	(Fujita, 2014)
Kurrichane thrush *(Turdus libonyana)*		Woodland	(Fujita, 2014)
Bat species			
Epomophorus wahlbergi	South Africa	National park	(Bleher et al., 2003; Bonaccorso et al., 2014)
Epomophorus crypturus	South Africa	National park	(Bonaccorso et al., 2014)
Rousettus aegyptiacus	Tanzania	Nature reserve	(Seltzer et al., 2013)
Stenonycteris lanosus	Tanzania		
Myonycteris angolensis	Tanzania		
Eidolon helvum	Tanzania		
Myonycteris relicta	Tanzania		

Epomophorus wahlbergi	Tanzania		
Epomophorus labiatus	Tanzania		
Primates			
Chimpanzee *(Pan troglodytes)*	Uganda	Forest reserve	(Tweheyo and Obua, 2001; Tweheyo and Lye, 2003)
	Uganda	National Park	(Potts et al., 2011; Watts et al., 2012)
	Uganda	Agricultural lands and fragmented Forest	(Reynolds and Reynolds, 1965; Conklin and Wrangham, 1994; Kuroda et al., 1996; Wrangham et al., 1996; McLennan, 2013; Bortolamiol et al., 2014; Kagoro-Rugunda and Hashimoto, 2015)
	Senegal		(Sugiyama and Koman, 1979; McGrew, 1988)
	Guinea		(Goodall, 1968; Sugiyama and Koman 1992)
	Tanzania	Woodland forest	(Nishida, 1968; Newton-Fisher, 1999)

	Congo	Forest	(Tutin and Fernandez, 1993)
	Rwanda		(Gross-Camp et al., 2009)
Red-tailed monkey (*Cercopithecus ascanius schmidti*)	Uganda	Forest reserve	(Tweheyo and Obua, 2001)
Blue monkey (*Cercopithecus mitis stuhlmanii*)	Uganda	Forest reserve	(Tweheyo and Obua, 2001)
Vervet monkey (*Cercopithecus pygerythrus)*	South Africa	Coastal forest	(Bleher et al., 2003)
Samango monkey (*Cercopithecus mitis)*	South Africa	Coastal forest	(Bleher et al., 2003)
Mountain gorilla (*Gorilla beringei beringei*)	Uganda	National Parks	(Ganas et al., 2004)
Other mammals			
Mutable sun squirrel (*Heliosciurus mutabilis*)	Malawi	Forest/Woodland	(Fujita, 2014)
Bushbabies (Galagidae)	Tanzania	National Parks	(Beentje and Mbago, 2007)
	Kenya		(Beentje, 1988)

Genet (*Genetta genetta*)	Tanzania		(Beentje and Mbago, 2007)
Mongoose (Herpestidae)	Tanzania		
Bushbuck (*Tragelaphus scriptus*)	Tanzania		
Duikers (*Cephalophini*)	Tanzania		
Bushpig (*Potamochoerus larvatus*)	Tanzania		
Suni (*Neotragus moschatus*)	Tanzania	National Parks	(Beentje and Mbago, 2007)
African civet (*Civettictis civetta*)	Tanzania	National Parks	(Beentje and Mbago, 2007)
	Ethopia	Forest reserve	(Habtamu et al., 2017)
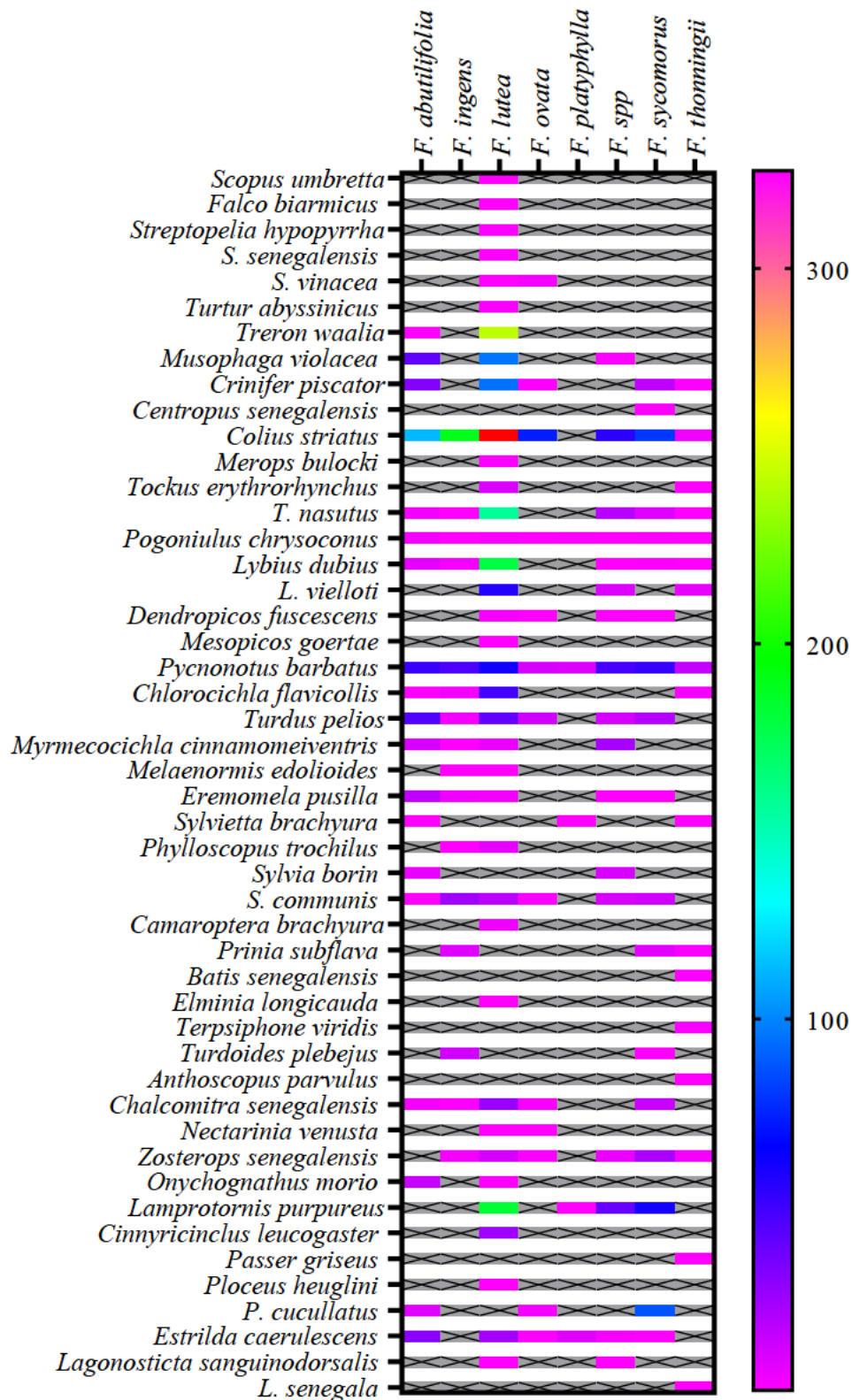
Fig. 2.3. Heat map of other fig-eating bird species interaction documented in West Africa. Matrix cells show the *Ficus*-bird pairs (column and rows corresponding to each species of *Ficus* and bird interaction with red colour indicating high visitation rate and pink to a blue colour indicating decreased number of visitations: as indicated in the numbered legend). (Visitation and nomenclature follows Daru et al. (2014) for land-use type- forest reserve. See Supplementary Table S2.8 for avian species).

Seed predators of *Ficus* spp. fruit have also been identified. For example, Bonaccorso et al. (2014), in their research, mentioned that Chacma baboons (*Papio ursinus*) and vervet monkeys (*Cercopithecus aethiops*) often ingest the fruits of *F. sycomorus* before the seeds are mature. Brown-headed Parrots (*Poicephalus cryptoxanthus*) were reported to open seeds in *Ficus* spp. fruit while ingesting the embryonic tissues (Bonaccorso et al., 2014). Another bird species that was reported to be a *Ficus* spp. seed predator is the African Green Pigeon (*Treron calva*) and Rose-ringed Parakeets (*Psittacula krameri*); they grind fig seeds against grit in their gizzards (Bonaccorso et al., 2014; Thabethe et al., 2015; Shivambu et al., 2021). Although, some researchers argued that some small seeds could escape being predated upon by animals like the above mentioned and they might still function as important, often long-distance, seed dispersers (Thabethe et al., 2015; Shiels et al., 2018; Klug et al., 2019; Shivambu et al., 2021)

2.4.3 Land-use changes in fig-frugivore interactions in Africa

Some of the leading causes of biodiversity loss are climate change, anthropogenic activities, and habitat fragmentation because of land-use change (Farwig et al., 2008; WWF, 2016; Chibesa and Downs, 2017). In South African forests, coastal *Ficus* spp. trees are found to continue to fruit throughout the year and produced the most significant biomass of fruits, especially when few or no alternative fruits were available for frugivore consumption (Herre et al., 2008). As such, *Ficus* spp. fruit may be critically important in helping frugivores survive resource bottlenecks, indicating that they may exert a disproportionately large influence on species composition or even morphological and sociological evolution. Habitat fragmentation and land-use modification are, therefore, exerting a negative impact on the abundance and presence of the keystone *Ficus* spp. fruit and affect frugivores that depend on these (Kirika et al., 2008). In the higher altitude Southern Mistbest Forest patches in South Africa, Hart et al. (2013) found that *Ficus* spp. trees were relatively rare and of low biomass.

High availability of fleshy fruited trees such as *Ficus* spp. trees in a fragmented or disturbed forest and a well-developed canopy stratum may facilitate the persistence of diverse bird and other frugivore communities (Lenz et al., 2011; Menke et al., 2012; Lenz et al., 2015). Trumpeter Hornbills were observed by Chibesa and Downs (2017) to prefer the fruits of *Ficus* spp. across forest-urban gradients, making *Ficus* spp. important indigenous trees in urban residential gardens for their persistence here. Their findings indicated that the removal of *Ficus* spp. as a result of further land modification might have a negative impact on the distribution and population of this bird species. Chibesa and Downs (2017), in their study, reported that although isolated *Ficus* spp. are avoided in a high housing density area, they act as stepping stones for forest mammals and large-bodied birds, especially in open habitat (Martin et al., 2009; Rafidison et al., 2020).

Forest disturbance had also been reported to have a negative effect on frugivore visitation rates of *Ficus* spp. fruit (Kirika et al., 2018). Bonaccorso et al. (2014) showed a strong dependence of epauletted fruits bats on *F. sycomorus* fruit as a food item throughout the year in Kruger National Park, South Africa, suggesting that the decline in crop production and abundance of this *Ficus* spp. may affect movements and population numbers of fruit here. A study by Compton and Greef (2020) along the Runde River and adjacent sections of major tributaries in Zimbabwe reported relatively low densities of *Ficus* spp. and crop mass as a result of water scarcity which could be a response to anthropogenic land-use changes in the study area. Therefore, the keystone function in that area was not realised; relatively few birds were observed on *Ficus* spp. trees, as they were only capable of supporting a small population of frugivores species.

2.4.4 Implications of land-use changes for fig-frugivore interactions

Anthropogenic land-use changes result in deforestation and habitat fragmentation affecting local climate, *Ficus* spp. presence, and forest regeneration, thereby reducing the keystone function of *Ficus* spp. and their potential to support populations of frugivorous animals (Compton and Greef, 2020). *Ficus* spp. trees have been recorded to retain their ecological significance even in more arid areas making their conservation very important and a great priority (Compton and Greef, 2020). The rapid increase in anthropogenic land-use activities has been recorded by several authors in Africa and other developing countries to be the most serious linked with the loss of biodiversity (Gibson et al., 2011). These land-use changes generally lead to the decline and loss of key dispersers in response to the loss of fruiting trees and alter the interaction structure in mutualistic networks (Kirika et al., 2008). Previously, it was known that species responded differently to anthropogenic changes in land-use because of different sensitivity to disturbances (Waston et al., 2018). While some species may take advantage of habitat modifications such as farmland or scattered trees within farmland, others may not. Anthropogenic land-use changes typically result in isolated and fewer *Ficus* trees, resulting in a decrease in vertebrate frugivore numbers and fruit removal and seed dispersal of *Ficus* spp. fruit (Kirika et al., 2008; Cordeiro et al., 2009). These results suggest that mutualistic interactions of keystone species can be particularly sensitive to human forest disturbance with potential long-term effects on the biodiversity of tropical forests. Consequently, this loss of frugivores can lower seed dispersal rates (Cordeiro et al., 2009). In contrast, frugivores and seed dispersal of the tree species *Prunus africana* were positively affected by anthropogenic disturbances in a Kenyan forest (Farwig et al., 2008).

However, decreasing forest fragment size could both, directly and indirectly, impact species persistence by lowering local population sizes and increasing edge effects as the relative amount of edge habitat are greater in smaller fragments (Farwig et al., 2008; de Lima

et al., 2013; Mahiga et al., 2019). This leads to increased forest isolation that undermines forest habitats' quality, resulting in an adverse impact on the population of trees and a key ecological process such as seed dispersal, altering the pivotal role of seed dispersers in the regeneration and restoration of plant communities across forest ecosystems globally (Farwig et al., 2008; de Lima et al., 2013; Mahiga et al., 2019).

2.5 Conclusions

An increase in habitat fragmentation and land-use changes can have a profound effect on frugivore abundance and the quantity of fruit removal. Some species such as *Ficus* spp. persist in degraded landscapes, depending on how fruit and seed characteristics interact with dispersers attributes (Rafidison et al., 2020). However, the abundance and diversity of fruiting trees and frugivore species generally decrease along the forest-urban gradient (Tweheyo and Obua, 2001; Tweheyo and Lye, 2003; Seltzer et al., 2013). Studies (e.g. Kirika et al., 2008) have shown that the loss of dispersers significantly affects the interactions between plants and their frugivorous species and subsequently affects plant recruitment. Large fruit size requiring large-gaped dispersers and species dispersed by deep forest frugivores, therefore experience reduced fruit removal and reduced dispersal within habitat fragments (Kirika et al., 2008; Laube et al., 2008; Schor et al., 2015). *Ficus* spp. tree abundance is a good predictor of the Trumpeter Hornbill across an urban-forest gradient in South Africa (Chibesa and Downs, 2017), chimpanzees in Uganda national parks and reserves (Tweheyo and Obua, 2001), for fruits bats in Eastern and southern Africa (Seltzer et al., 2013; Bonaccorso et al., 2014) and for many other bird species in Africa (Burrows and Burrows, 2003; Daru et al., 2015). Our present review suggests that declines in the population of *Ficus* spp. trees as a result of land-use changes, demand for forest products, illegal timber harvesting, and urbanisation may force vertebrate frugivores such as primates, bats, and birds to shift and migrate, from their natural habitats to

more vulnerable habitats; including areas bordered by human settlements which may lead to human-wildlife conflicts, and the disappearance of certain local frugivores species.

2.5.1 Conservation of figs and future direction to enhance its frugivore interaction

As a result of the asynchronous fruiting pattern of *Ficus* spp., many animal species and individuals have been observed to feed on figs. Given this, conservation and management programmes that will enhance the conservation of *Ficus* spp. and conserve vertebrate frugivores that depend on their fruits must be put in place. Further research is required on the role that *Ficus* spp. play in regenerating economically and medicinal useful plant resources in rural areas and, the impacts of anthropogenic land-use changes on *Ficus* spp. populations and adverse impacts on frugivores in other to make an essential decision on conservation of *Ficus* spp., both in the natural forest under high human pressure and in the urban mosaic areas. Planting of keystone *Ficus* spp. for restoration projects act as a seed bank reducing the cost involved in seed collection because of their ability to produce large fruit crops all year round. They also serve as habitat corridors and enhanced landscape connectivity for plants and frugivores, accelerating recovery of degraded land. *Ficus* spp. trees planted in urban areas for urban greening will also attract certain frugivore species that depend on fig fruit, especially in periods of food scarcity.

2.6 Declarations

Author contributions

Conceptualisation of the study was done by IAR and CTD. methodology, IAR.; data collection, IAR writing—original draft preparation, IAR.; writing—review and editing, CTD. and IAR.; supervision, CTD.; funding acquisition, CTD and NRF-TWAS. All authors have read and agreed to the published version of the manuscript.

Conflicts of interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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2.8 Supplementary information

Boolean search: We performed a boolean search on Web of science, Google scholar and Wiley online library

⬇

1. Boolean operators query: (*Ficus** and frugivores*) OR (figs* and frugivores*) OR (*Ficus** seed dispersal* and seed dispersers*) OR (figs* and seed dispersers*) AND (Land use* OR Urban* forest*) AND (Africa*)
2. There was no restriction in the publication years

⬇

Result of Boolean search

1. Web of Science: 392
2. Google Scholar: 4590
3. Wiley Online Library: 6301

⬇

We first searched Web of Science pages, Wiley Online Library and Google Scholar. We stopped searching when searches resulted in no new publications. We removed publications that are duplicate of other searches. We then manually evaluated the title, abstract and discussion of each publication to determine its relevance to our research. We remove those that are not relevant and retained those that are relevant: see Figure 2.1

⬇

Our topics of interest includes: Figs as diets to frugivores, foraging movement, seed dispersals, Figs-frugivore visitation, Urban-forest gradient of figs distribution and its frugivores in Africa

⬇

Result screening: 295

Total number of publications in this review: 70 (Figure 2.1, Supplementary Table S2.1)

Supplementary Figure S2.1: Boolean search flow chart for literature review
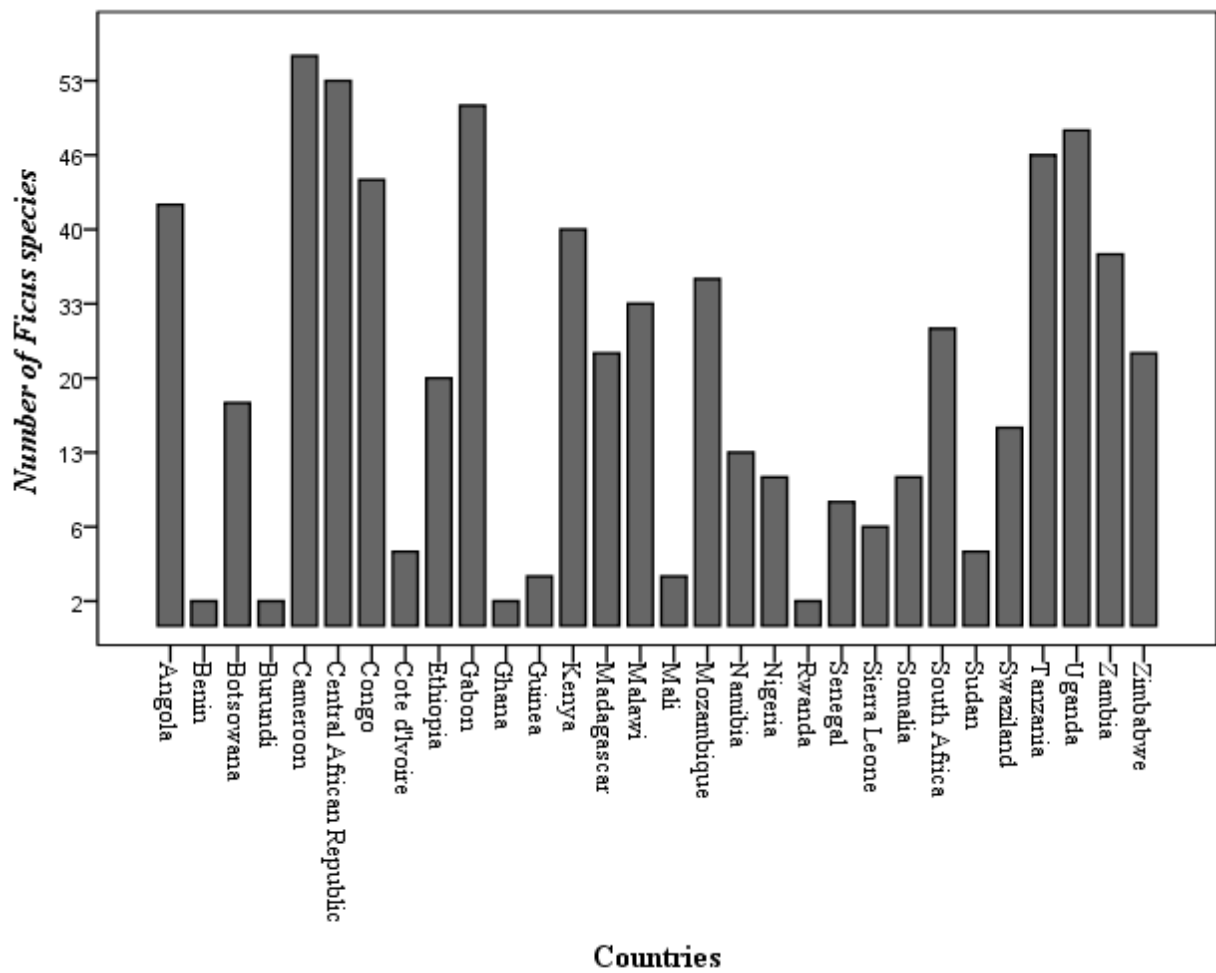
Supplementary Figure S2.2. Number of *Ficus* species record per African country (data from Berg & Hijman, 1989; Berg & Wiebes, 1992; Burrows & Burrows, 2003; Luke, 2005; Daru et al., 2014; Van Noort and Rasplus, 2020).

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Supplementary Table S2.2 Distribution of fig tree species in southern Africa (after Berg, 1990, 1991; Burrows and Burrows, 2003; Van Noort et al. 2007; Van Noort and Rasplus 2020)

Ficus species	Angola	Botswana	Mozambique	Namibia	South Africa	Swaziland	Zambia	Zimbabwe
Subgenus (Sycidium)								
Section (Sycidium)								
1. *F. exasperata* Vahl	*		*					*
2. *F. asperifolia* Miq	*						*	
3. *F. pygmaea* Hiern	*	*		*			*	
4. *F. capreifolia* Delile	*	*	*	*	*	*	*	*
5. *F. pachyclada pachyclada* Baker								
Subgenus (Sycomorus)								
6. *F. sycomorus sycomorus* L.	*	*	*	*	*	*	*	*
7. *F. sycomorus gnaphalocarpa* (Miq.)	*		*		*		*	

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Species								
8. *F. sur* Forssk.	*	*	*		*	*	*	*
9. *F. vallis-choudae* Delile	*		*				*	*
10. *F. tiliifolia*								
11. *F. polyphlebia* Baker								
12. *F. botryoides* Baker								
13. *F. mucuso* Ficalho	*							

Subgenus (Pharmacosycea)

Section (Oreosycea)

Subsection(pedunculatea)

Species								
14. *F. dicranostyla* Mildbr	*						*	
15. *F. variifolia* Warb.	*							

Subgenus (Urostigma)

Section (Urostigma)

Subsection (Urostigma)

Species								
16. *F. verruculosa Warb.*	*	*	*	*	*		*	*
17. *F. salicifolia (Vahl) Berg*		*	*		*	*	*	*

18. *F. cordata cordata Thunb.*	*	*		*	*			
19. *F. ingens (Miq.) Miq.*	*	*	*	*	*	*	*	*
20. *F. cordata lecardii (Warb.) Berg*								
Subsection (Conosyscea)								
21. *F. microcarpa Linnaeus*					*			
Section (Galoglychia)								
Subsection (Galoglychia)								
22. *F. lutea Vahl*	*		*	*	*	*	*	*
23. *F. saussureana DC.*								
Subsection (Platyphyllae)								
24. *F. bussei Mildbr. and Burret*			*				*	*
25. *F. recurvata De Wildeman*	*							
26. *F. wakefieldii Hutch.*							*	
27. *F. glumosa Delile*	*	*	*	*	*	*	*	*
28. *F. stuhlmannii Warb.*			*		*	*	*	*

Species								
29. *F. nigropunctata Mildbr. and Burret*		*	*					*	*
30. F. tettensis Hutch.		*	*		*			*	*
31. F. muelleriana Berg			*						
32. *F. abutilifolia (Miq.) Miq*		*	*		*	*		*	*
33. *F. trichopoda Baker*			*		*			*	
Subsection (Chlamydodorae)									
34. *F. fischeri Mildbr. and Burret*	*	*	*	*				*	*
35. *F. craterostoma Mildbr. and Burret*	*		*		*	*		*	*
36. *F. linqua depauperata (Sim) C.C. Berg*			*		*				
37. *F. natalensis natalensis Hochs*		*	*		*			*	

Species								
38. *F. natalensis leprieurii (Miq.) C.C. Berg*	*						*	
39. *F. natalensis graniticola Burrows*					*			*
40. *F. burtt-davyi Hutch.*			*		*	*		
41. *F. ilicina (Sonder) Miq*	*			*	*			
42. *F. rokko Warb. and Schweinf. in Warb.*	*		*					*
43. *F. psilopoga Ficalho*	*						*	
44. *F. persicifolia Warb*	*						*	
45. *F. petersii Warb.*	*	*	*	*	*	*	*	*
46. *F. burkei (Miq.) Miq.*		*	*	*	*	*	*	*

Subsection (Crassicostae)

Species								
47. *F. usambarensis Warb*			*				*	
48. *F. elasticoides De Wild.*	*							
49. *F. burretiana Hutch.*								

Species					
50. *F. pseudomangifera Hutch.*	*				

Subsection (Cyathistipulae)

Species					
51. *F. ardisioides camptoneura (Mildbr.) C.C. Berg*				*	
52. *F. cyathistipula cyathistipula Warb.*	*	*		*	
53. *F. scassellatii scassellatii Pamp.*		*		*	*
54. *F. barteri Sprague*	*			*	
55. *F. abscondita C.C Berg*					
56. *F. conraui Warb.*	*				
57. *F. densistipulata De Wild.*	*				
58. *F. subcostata De Wild*	*				
59. *F. ottoniifolia macrosyce C.C. Berg*	*			*	
60. *F. tremula tremula Warb.*		*	*		

Species							
61. *F. polita polita Vahl*	*		*		*	*	
62. *F. polita brevipedunculata C.C. Berg*							*
63. *F. bizanae Hutch. and Burtt-Davy*					*		
64. *F. modesta White*			*				*
65. *F. chirindensis C.C. Berg*			*				*
66. *F. sansibarica sansibarica Warb.*			*		*	*	*	*
67. *F. sansibarica macrosperma (Mildbr. and Burret)*	*						*
68. *F. bubu Warb.*	*		*	*	*	*		*
69. *F. ovata Vahl*	*	*	*				*
70. *F. ottoniifolia ottoniifolia (Miq.) Miq.*							

71. *F. tremula kimuenzensis (Warb) C.C Berg*	*	
72. *F. artocarpoides Warb.*	*	
73. *F. umbellata Vahl*	*	
74. *F. ottoniifolia lucanda (Ficalho) C.C. Berg*	*	

Supplementary Table S2.3. Distribution of fig tree species in West Africa (after Berg, 1990, 1991; Burrows and Burrows, 2003; Daru et al., 2014; Van Noort & Rasplus 2020)

Ficus species	Benin	Cote d'Ivoire	Ghana	Guinea	Mali	Nigeria	Senegal	Sierra Leone
Subgenus (Sycidium)								
Section (Sycidium)								
1. *F. exasperata Vahl*			*				*	
2. *F. capreifolia Delile*							*	
Subgenus (Sycomorus)								
3. *F. sycomorus sycomorus L.*	*							
4. *F. sur Forssk.*			*			*	*	
5. *F. vogeliana (Miq) Miq*			*					
Subgenus (Pharmacosycea)								
Section (Oreosycea)								
Subsection(pedunculatea)								
6. *F. dicranostyla Mildbr*					*			
7. *F. variifolia Warb.*								*

Section (Urostigma)

Subsection (Urostigma)

8. *F. verruculosa Warb.*				*	
9. *F. cordata cordata Thunb.*					*
10. *F. ingens (Miq.) Miq.*	*				*
11. *F. cordata lecardii (Warb.) Berg*					*

Subsection (Conosyscea)

12. *F. benjamina*				*	
13. *F. microcarpa Linnaeus*		*			

Section (Galoglychia)

Subsection (Galoglychia)

14. *F. lutea Vahl*			*		

Subsection (Platyphyllae)

15. *F. glumosa Delile*				*	*
16. *F. abutilifolia (Miq.) Miq*		*		*	

17. F. trichopoda Baker				
18. F. platyphylla Delile			*	
Subsection (Chlamydodorae)				
19. F. craterostoma Mildbr. &				
Burret	*	*		*
20. F. natalensis natalensis Hochs			*	
21. F. thonningii	*		*	
22. F. kamerunensis Mildbr. &				
Burret				*
Subsection (Crassicostae)	*			
23. F. orepdryadum Mildbr.			*	
Subsection (Cyathistipulae)				
24. F. conraui Warb.				*
25. F. lyrata Warb				*
26. F. sagittifolia Mildbr. &Burret		*		
27. F. polita polita Vahl	*	*	*	

28. *F. ovata Vahl*			*	
29. *F. tremula kimuenzensis (Warb)*				
C.C Berg			*	
30. *F. artocarpoides Warb.*				
31. *F. umbellata Vahl*	*		*	*

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Supplementary Table S2.4. Distribution of fig tree species in Central and Northern Africa (after Berg, 1990, 1991; Burrows and Burrows, 2003; Van Noort and Rasplus 2020)

Ficus species	Central African Republic	Congo	Gabon	Cameroon	Sudan
Subgenus (Sycidium)					
Section (Sycidium)					
1. *F. exasperata Vahl*	*	*	*	*	
2. *F. asperifolia Miq*	*	*	*	*	
3. *F. pygmaea Hiern*					
4. *F. capreifolia Delile*	*			*	
Subgenus (Sycomorus)					
5. *F. sycomorus sycomorus L.*				*	
6. *F. sycomorus gnaphalocarpa (Miq.)*	*				
7. *F. sur Forssk.*	*	*	*	*	
8. *F. vallis-choudae Delile*	*			*	
9. *F. mucuso Ficalho*	*	*	*	*	

	1	2	3	4	5
10. F. vogeliana (Miq) Miq	*		*	*	*
Subgenus (Pharmacosycea)					
Section (Oreosycea)					
Subsection(pedunculatea)					
11. F. dicranostyla Mildbr	*		*	*	*
12. F. variifolia Warb.	*		*	*	*	*
Subgenus (Urostigma)					
Section (Urostigma)					
Subsection (Urostigma)					
13. F. verruculosa Warb.	*				*
14. F. ingens (Miq.) Miq.	*		*	*	*
15. F. cordata lecardii (Warb.) Berg	*				*
Subsection (Conosyscea)					
Subsection (Galoglychia)					
16. F. lutea Vahl	*		*	*	*
17. F. saussureana DC.	*				*	*

	C1	C2	C3	C4	C5
18. F. chlamydocarpa chlamydocarpa Mildbr. &Burret				*	

Subsection (Platyphyllae)

	C1	C2	C3	C4	C5
19. F. bussei Mildbr. and Burret					
20. F. recurvata De Wildeman	*	*	*	*	
21. F. jansii Boutique			*	*	
22. F. populifolia Vahl	*			*	
23. F. wakefieldii Hutch.					
24. F. glumosa Delile	*			*	
25. F. abutilifolia (Miq.) Miq	*			*	
26. F. trichopoda Baker	*	*	*	*	
27. F. platyphylla Delile	*			*	
28. F. vasta Forsk.					*

Subsection (Chlamydodorae)

	C1	C2	C3	C4	C5
29. F. craterostoma Mildbr. and Burret	*	*	*	*	*

30. *F. linqua depauperata (Sim) C.C. Berg*				*
31. *F. natalensis leprieurii (Miq.) C.C. Berg*	*	*	*	*
32. *F. rokko Warb. and Schweinf. in Warb.*	*	*	*	*
33. *F. psilopoga Ficalho*	*	*	*	*
34. *F. persicifolia Warb*	*	*	*	*
35. *F. calyptrata Vahl*	*	*	*	*
36. *F. amadiensis*	*	*	*	*
37. *F. kamerunensis Mildbr. &Burret*	*	*	*	*
38. *F. linqua linqua De Wild & T. Durand*	*	*	*	

Subsection (Crassicostae)

39. *F. elasticoides De Wild.*	*	*	*	*

40. F. burretiana Hutch.	*	*	*	*
41. F. orepdryadum Mildbr.			*	*
42. F. pseudomangifera Hutch.	*	*	*	*
43. F. adolfi-friderici mildbr.	*	*	*	*
44. F. louisii Boutique & J. Leonard	*	*	*	*
45. F. loenensis Hutch			*	*

Subsection (Cyathistipulae)

46. F. ardisioides camptoneura (Mildbr.) C.C. Berg	*	*	*	*
47. F. cyathistipula cyathistipula Warb.	*	*	*	*
48. F. barteri Sprague	*	*	*	*
49. F. abscondita C.C Berg			*	*
50. F. conraui Warb.	*	*	*	*
51. F. preussii Warb	*	*	*	*
52. F. cyathistipula pringsheimaiana (Braun &K. Shum.) C.C. berg			*	*

53. *F. cyathistipuloides De Wild.*			*	*
54. *F. densistipulata De Wild.*	*	*	*	*
55. *F. subcostata De Wild*	*	*	*	*
56. *F. lyrata Warb*				*
57. *F. sagittifolia Mildbr. &Burret*				*
58. *F. subsagittifolia C.C. Berg*			*	*
59. *F. wildmaniana de Wild. & T. Durand*	*	*	*	*
60. *F. oresbia C.C. Berg*				*
61. *F. tesselata Warb.*			*	
Subsection (Caulocarpae)				
62. *F. polita polita Vahl*	*	*	*	*
63. *F. sansibarica macrosperma (Mildbr. and Burret)*	*	*	*	*
64. *F. bubu Warb.*	*	*	*	*
65. *F. ovata Vahl*	*	*	*	*

66. *F. ottoniifolia ottoniifolia (Miq.)*				
Miq.	*	*	*	*
67. *F. tremula kimuenzensis (Warb)*				
C.C Berg	*	*	*	*
68. *F. artocarpoides Warb.*	*	*	*	*
69. *F. umbellata Vahl*	*	*	*	*
70. *F. dryepondtiana De Wild.*	*	*	*	*
71. *F. tremula acuta (De Wild.) C.C.*				
Berg		*		
72. *F. ottoniifolia lucanda (Ficalho)*				
C.C. Berg	*	*	*	

Supplementary Table S2.5. Distribution of fig tree species in East Africa (after Berg, 1990, 1991; Burrows and Burrows, 2003; Van Noort and Rasplus 2020)

Ficus species	Burundi	Ethiopia	Kenya	Madagascar	Malawi	Rwanda	Tanzania	Uganda	Somalia
Subgenus (*Ficus*)									
Section (*Ficus*)									
Subsection (*Ficus*)									
1. *F. palmata Forsk.*		*							*
Subgenus (Sycidium)									
Section (Sycidium)									
2. *F. exasperata Vahl*		*	*		*		*	*	
3. *F. asperifolia Miq*		*	*				*	*	
4. *F. pygmaea Hiern*									
5. *F. capreifolia Delile*		*	*		*		*	*	*
6. *F. pachyclada pachyclada Baker*				*					

	Col1	Col2	Col3	Col4	Col5	Col6	Col7
7. F. pachyclada arborera (Parrier) C.C. Berg			*				
8. F. bojeri Baker			*				
9. F. brachyclada Barker			*				
10. F. politoria Lam.			*				

Subgenus (Sycomorus)

	Col1	Col2	Col3	Col4	Col5	Col6	Col7
11. F. sycomorus sycomorus L.	*	*	*	*	*	*	*
12. F. sycomorus gnaphalocarpa (Miq.)				*			
13. F. sur Forssk.	*	*		*	*	*	*
14. F. vallis-choudae Delile	*	*		*	*	*	
15. F. sycomorus ``sakalavarum''			*				
16. F. tiliifolia			*				
17. F. polyphlebia Baker			*				
18. F. botryoides Baker			*				
19. F. mucuso Ficalho	*				*	*	

20. F. vogeliana (Miq) Miq						*	
21. F. torrentium Perrier			*				
22. F. trichoclada Baker			*				
23. F. karthalensis			*				

Subgenus (Pharmacosycea)

Section (Oreosycea)

Subsection(pedunculatea)

24. F. dicranostyla Mildbr	*					*	
25. F. variifolia Warb.					*	*	
26. F. assimilis Baker			*				
27. F. ampana Berg			*				

Subgenus (Urostigma)

Section (Urostigma)

Subsection (Urostigma)

28. F. verruculosa Warb.		*		*	*	*	
29. F. salicifolia (Vahl) Berg	*	*		*	*	*	*

Species							
30. F. cordata cordata Thunb.							
31. F. ingens (Miq.) Miq.	*	*		*	*	*	*
32. F. cordata lecardii (Warb.) Berg							
33. F. madagascariensis C.C. Berg			*				

Subsection (Conosyscea)

Species							
34. F. menabeensis Parrier			*				
35. F. humbertii Berg			*				

Section (Galoglychia)

Subsection (Galoglychia)

Species							
36. F. lutea Vahl	*	*	*	*	*	*	
37. F. saussureana DC.		*			*	*	

Subsection (Platyphyllae)

Species							
38. F. bussei Mildbr. and Burret		*		*	*		
39. F. populifolia Vahl	*	*			*	*	*
40. F. wakefieldii Hutch.		*			*	*	
41. F. glumosa Delile	*	*		*	*	*	*

Species							
42. F. stuhlmannii Warb.		*		*	*	*	
43. F. nigropunctata Mildbr. and Burret		*		*	*		
44. F. tettensis Hutch.				*			
45. F. muelleriana Berg							
46. F. abutilifolia (Miq.) Miq	*	*		*	*	*	
47. F. trichopoda Baker			*	*	*	*	
48. F. platyphylla Delile	*					*	*
49. F. vasta Forsk.	*	*				*	*
50. F. grevei Baill.			*				
51. F. rubra Vahl			*				
52. F. marmorata Baker			*				
53. F. bivalvata Perrier			*				

Subsection (Chlamydodorae)

54. F. fischeri Mildbr. and Burret				*	*		

Species						
55. *F. craterostoma Mildbr. and Burret*		*	*	*	*	
56. *F. linqua depauperata (Sim) C.C. Berg*		*		*		
57. *F. natalensis natalensis Hochs*		*	*	*	*	
58. *F. rokko Warb. and Schweinf. in Warb.*	*	*	*	*	*	
59. *F. psilopoga Ficalho*				*	*	
60. *F. persicifolia Warb*				*	*	
61. *F. petersii Warb.*		*	*	*		
62. *F. burkei (Miq.) Miq.*		*	*	*	*	
63. *F. thonningii*						*
64. *F. amadiensis*		*		*	*	
65. *F. faulkneriana C.C Berg*		*		*		
66. *F. linqua linqua De Wild & T. Durand*					*	

67. *F. antandronarum antandronarum (Perrier) Berg*		*				
68. *F. reflexa reflexa Thunb.*		*				

Subsection (Crassicostae)

69. *F. usambarensis Warb*	*			*		
70. *F. orepdryadum Mildbr.*					*	*
71. *F. pseudomangifera Hutch.*						*

Subsection (Cyathistipulae)

72. *F. cyathistipula cyathistipula Warb.*	*			*	*	
73. *F. scassellatii scassellatii Pamp.*	*		*	*		*
74. *F. barteri Sprague*					*	
75. *F. abscondita C.C Berg*						
76. *F. conraui Warb.*					*	
77. *F. preussii Warb*					*	
78. *F. densistipulata De Wild.*					*	

Species					
79. F. wildmaniana de Wild. & T. Durand					*
80. F. scassellatii thikaensis C.C Berg	*				
Subsection (Caulocarpae)					
81. F. ottoniifolia ulugurensis (Mildbr and Burret) C.C. Berg	*		*	*	*
82. F. ottoniifolia macrosyce C.C. Berg					*
83. F. tremula tremula Warb.	*		*	*	
84. F. polita polita Vahl	*	*	*	*	*
85. F. polita brevipedunculata C.C. Berg			*	*	
86. F. modesta White			*		
87. F. chirindensis C.C. Berg	*		*	*	*

Species							
88. *F. sansibarica sansibarica Warb.*			*	*		*	
89. *F. sansibarica macrosperma (Mildbr. & Burret)*			*				*
90. *F. bubu Warb.*			*	*		*	*
91. *F. ovata Vahl*		*	*	*		*	*
92. *F. ottoniifolia ottoniifolia (Miq.) Miq.*							*
93. *F. artocarpoides Warb.*						*	*
94. *F. umbellata Vahl*		*					
95. *F. tremula acuta (De Wild.) C.C. Berg*	*		*		*	*	*
96. *F. ottoniifolia lucanda (Ficalho) C.C. Berg*						*	*

Supplementary Table S2.6. Number of *Ficus* species record per African country updated from Figweb.

	Country	No. of *Ficus* species	References
1.	Angola	41	Berg et al., 1985; Berg & Wiebes, 1992; Van Noort & Rasplus, 2020
2.	Benin	2	Van Noort & Rasplus, 2020
3.	Botswana	17	Burrows & Burrows, 2003; Setshogo, 2005; Van Noort & Rasplus, 2020
4.	Burundi	2	Berg, 1988; Berg & Wiebes, 1992; Bouček et al., 1981; Van Noort & Rasplus, 2020
5.	Cameroon	63	Berg et al., 1985; Berg & Wiebes, 1992; Ebika et al., 2015; 2018; Van Noort & Rasplus, 2020
6.	The Central African Republic	53	Van Noort & Rasplus, 2020
7.	Congo	4	Berg, 1988; Berg & Wiebes, 1992; Bouček et al., 1981; Van Noort & Rasplus, 2020
8.	Cote d'Ivoire	44	Berg, 1988; Berg & Wiebes, 1992; Bouček et al., 1981; Van Noort & Rasplus, 2020
9.	Ethiopia	20	Friis, 1990; Van Noort & Rasplus, 2020.
10.	Gabon	51	Berg, et al., 1984; Van Noort & Rasplus, 2020

11.	Ghana	3	Van Noort & Rasplus, 2020
12.	Guinea	2	Van Noort & Rasplus, 2020
13.	Kenya	40	Berg & Hijman, 1989; Beentje, 1994; van Noort & Compton, 1999; Burrows & Burrows, 2003; Luke, 2005; Van Noort & Rasplus, 2020
14.	Madagascar	27	Berg, 1986; Berg & Wiebes, 1992; Van Noort & Rasplus, 2020
15.	Malawi	33	Burrows & Burrows, 2003; Van Noort & Rasplus, 2020
16.	Mali	3	Van Noort & Rasplus, 2020
17.	Mozambique	36	Berg & Wiebes, 1992; Burrows & Burrows, 2003; Da Silva et al., 2004; van Noort et al., 2007; Van Noort & Rasplus, 2020
18.	Namibia	13	Van Jaarsveld & Voight 2003; Van Noort & Rasplus 2020
19.	Nigeria	12	Berg, 1988; Berg & Wiebes, 1992; Bouček et al., 1981; Daru et al., 2014; Van Noort & Rasplus, 2020
20.	Rwanda	2	Van Noort & Rasplus, 2020
21.	Senegal	9	Van Noort & Rasplus, 2020
22.	Sierra Leone	6	Van Noort & Rasplus, 2020
23.	Somalia	12	Friis, 1990; Van Noort & Rasplus, 2020
24.	South Africa	28	Burrows & Burrows, 2003; Bleher et al., 2004; Setshogo, 2005; Van Noort & Rasplus, 2020
25.	Sudan	4	Van Noort & Rasplus, 2020

26.	Swaziland	16	Van Noort & Rasplus, 2020
27.			(Berg & Hijman, 1989; Beentje, 1994; van Noort & Compton, 1999; Burrows & Burrows, 2003; Beentje & Mbago, 2007; Van Noort &
	Tanzania	46	Rasplus, 2020
28.			Berg & Hijman, 1989; Berg & Hijman, 1989; van Noort & Compton, 1999; Burrows & Burrows, 2003; van Noort et al., 2007; Van Noort &
	Uganda	50	Rasplus, 2020
29.			Berg et al., 1985; Dowsett-Lemaire, 1985; Burrows & Burrows, 2003;
	Zambia	39	Van Noort & Rasplus, 2020
30.	Zimbabwe	27	Van Noort & Rasplus, 2020

Supplementary Table S2.7. Distribution of *Ficus* spp. tree species across African as updated from Figweb and the number of countries found across each African region (Van Noort and Rasplus, 2020). (Note: southern Africa includes Angola, Botswana, Mozambique, Namibia, South Africa, Swaziland, Zambia, Zimbabwe; East Africa includes Burundi, Ethiopia, Kenya, Madagascar, Malawi, Rwanda, Tanzania, Uganda, Somalia; Central and North Africa include Central African Republic, Congo, Gabon, Cameroon, Sudan; and West Africa includes Benin, Cote d'lvoire, Ghana, Guinea, Mali, Nigeria, Senegal).

	Number of countries with presence			
Ficus **species**	**Southern Africa**	**East Africa**	**Central/North Africa**	**West Africa**
F. palmata Forsk.	0	2	0	0
F. exasperata Vahl	3	5	4	2
F. asperifolia Miq	2	4	4	0
F. pygmaea Hiern	4	0	0	0
F. capreifolia Delile	8	6	2	1
F. pachyclada pachyclada baker	0	1	0	0
F. pachyclada arborera (Parrier) C.C. Berg	0	1	0	0
F. bojeri Baker	0	1	0	0
F. brachyclada Barker	0	1	0	0
F. politoria Lam.	0	1	0	0
F. sycomorus sycomorus L.	8	7	1	1
F. sycomorus gnaphalocarpa (Miq.)	4	1	1	0
F. sur Forssk.	7	6	4	3
F. vallis-choudae Delile	4	5	2	0
F. sycomorus ``sakalavarum''	0	1	0	0
F. tiliifolia	0	1	0	0
F. polyphlebia Baker	0	1	0	0
F. botryoides Baker	0	1	0	0
F. mucuso Ficalho	1	3	4	0
F. vogeliana (Miq) Miq	0	1	4	1
F. torrentium Perrier	0	1	0	0
F. trichoclada Baker	0	1	0	0
F. karthalensis	0	1	0	0
F. dicranostyla Mildbr	2	2	4	1
F. variifolia Warb.	1	2	5	1
F. assimilis Baker	0	1	0	0
F. ampana Berg	0	1	0	0
F. verruculosa Warb.	7	4	2	1
F. salicifolia (Vahl) Berg	6	6	0	0
F. cordata cordata Thunb.	4	0	0	1
F. ingens (Miq.) Miq.	8	6	4	2
F. cordata lecardii (Warb.) Berg	0	0	2	1
F. madagascariensis C.C. Berg	0	1	0	0
F. menabeensis Parrier	0	1	0	0

F. humbertii Berg	0	1	0	0
F. benjamina	0	0	0	1
F. microcarpa Linnaeus	1	0	0	1
F. lutea Vahl	7	6	4	1
F. saussureana DC.	0	3	3	0
F. chlamydocarpa chlamydocarpa Mildbr. & Burret	0	0	1	0
F. bussei Mildbr. and Burret	3	3	0	0
F. recurvata De Wildeman	1	0	4	0
F. jansii Boutique	0	0	2	0
F. populifolia Vahl	0	5	2	0
F. wakefieldii Hutch.	1	3	0	0
F. glumosa Delile	8	6	2	2
F. stuhlmannii Warb.	5	4	0	0
F. nigropunctata Mildbr. and Burret	4	3	0	0
F. tettensis Hutch.	5	1	0	0
F. muelleriana Berg	1	0	0	0
F. abutilifolia (Miq.) Miq	6	5	2	2
F. trichopoda Baker	3	4	4	0
F. platyphylla Delile	0	3	2	1
F. vasta Forsk.	0	4	1	0
F. grevei Baill.	0	1	0	0
F. rubra Vahl	0	1	0	0
F. marmorata Baker	0	1	0	0
F. bivalvata Perrier	0	1	0	0
F. fischeri Mildbr. and Burret	6	2	0	0
F. craterostoma Mildbr. and Burret	6	4	5	3
F. linqua depauperata (Sim) C.C. Berg	2	2	1	0
F. natalensis natalensis Hochs	4	4	0	1
F. natalensis leprieurii (Miq.) C.C. Berg	2	0	4	0
F. natalensis graniticola Burrows	2	0	0	0
F. burtt-davyi Hutch.	3	0	0	0
F. ilicina (Sonder) Miq	3	0	0	0
F. rokko Warb. and Schweinf. in Warb.	3	5	4	0
F. psilopoga Ficalho	2	2	4	0
F. persicifolia Warb	2	2	4	0
F. petersii Warb.	8	3	0	0
F. burkei (Miq.) Miq.	7	4	0	0
F. thonningii	0	1	0	2
F. calyptrata Vahl	0	0	4	0
F. amadiensis	0	3	4	0
F. kamerunensis Mildbr. & Burret	0	0	4	1
F. faulkneriana C.C Berg	0	2	0	0
F. linqua linqua De Wild & T. Durand	0	1	3	0
F. antandronarum antandronarum (Perrier) Berg	0	1	0	0
F. reflexa reflexa Thunb.	0	1	0	0

F. usambarensis Warb	2	2	0	0
F. elasticoides De Wild.	1	0	4	0
F. burretiana Hutch.	0	0	4	0
F. orepdryadum Mildbr.	0	3	2	0
F. pseudomangifera Hutch.	1	1	4	0
F. adolfi-friderici mildbr.	0	0	4	0
F. louisii Boutique & J. Leonard	0	0	4	0
F. loenensis Hutch	0	0	2	0
F. ardisioides camptoneura (Mildbr.) C.C. Berg	1	0	4	0
F. cyathistipula cyathistipula Warb.	3	3	4	0
F. scassellatii scassellatii Pamp.	3	4	0	0
F. barteri Sprague	2	1	4	0
F. abscondita C.C Berg	0	0	2	0
F. conraui Warb.	1	1	4	1
F. preussii Warb	0	1	4	0
F. cyathistipula pringsheimaiana (Braun &K. Shum.) C.C. berg	0	0	2	0
F. cyathistipuloides De Wild.	0	0	2	0
F. densistipulata De Wild.	1	1	4	0
F. subcostata De Wild	1	0	4	0
F. lyrata Warb	0	0	1	1
F. sagittifolia Mildbr. & Burret	0	0	1	1
F. subsagittifolia C.C. Berg	0	0	2	0
F. wildmaniana de Wild. & T. Durand	0	1	4	0
F. oresbia C.C. Berg	0	0	1	0
F. scassellatii thikaensis C.C Berg	0	1	0	0
F. tesselata Warb.	0	0	1	0
F. ottoniifolia ulugurensis (Mildbr and Burret) C.C. Berg	0	4	0	0
F. ottoniifolia macrosyce C.C. Berg	2	1	0	0
F. tremula tremula Warb.	2	3	0	0
F. polita polita Vahl	4	5	4	3
F. polita brevipedunculata C.C. Berg	1	2	0	0
F. bizanae Hutch. and Burtt-Davy	1	0	0	0
F. modesta White	2	1	0	0
F. chirindensis C.C. Berg	2	4	0	0
F. sansibarica sansibarica Warb.	5	3	0	0
F. sansibarica macrosperma (Mildbr. and Burret)	2	2	4	0
F. bubu Warb.	6	4	4	0
F. ovata Vahl	4	5	4	1
F. ottoniifolia ottoniifolia (Miq.) Miq.	0	1	4	0
F. tremula kimuenzensis (Warb) C.C Berg	1	0	4	1
F. artocarpoides Warb.	1	2	4	0
F. umbellata Vahl	1	1	4	3
F. dryepondtiana De Wild.	0	0	4	0
F. tremula acuta (De Wild.) C.C. Berg	0	5	1	0

| *F. ottoniifolia lucanda (Ficalho) C.C. Berg* | 1 | 2 | 3 | 0 |

Supplementary Table S2.8. Other fig-eating bird species documented in West Africa. Nomenclature followed Daru et al. (2014), Land-use Type- Forest Reserve. (Note: Fa- *F. abutilifolia*, Fi- *F. ingens*, Fl- *F. lutea*, Fo- *F. ovata*, Fp- *F. platyphylla*, Fsp- F. species, Fsy- *F. sycomorus* and Ft- *F. thonningii).*

Birds	Fig species visited/number of visits							
	Fa	*Fi*	*Fl*	*Fo*	*Fp*	*F*sp	*Fsy*	*Ft*
Scopidae								
Scopus umbretta Hamerkop			1					
Falconidae								
Falco biarmicus Lanner Falcon			1					
Columbidae								
Streptopelia hypopyrrha Adamawa Turtle Dove			2					
S. senegalensis Laughing Dove			1					
S. vinacea Vinaceous Dove			1	4				
Turtur abyssinicus Black-billed Wood Dove			3					
Treron waalia Bruce's Green Pigeon	1		244					
Musophagidae								
Musophaga violacea Violet Turaco	41		96			2		
Crinifer piscator Western Grey Plantain-eater	32		95	2			17	1

Cuculidae

Centropus senegalensis Senegal Coucal						1	

Coliidae

Colius striatus Speckled Mousebird	113	189	326	73	55	80	5

Meropidae

Merops bulocki Red-throated Bee-eater			2				

Bucerotidae

Tockus erythrorhynchus Red-billed Hornbill			10				1
T. nasutus African Grey Hornbill	4	1	157		19	9	1

Lybiidae

Pogoniulus chrysoconus Yellow-fronted Tinkerbird	4	1	3	1	2	1	2	1
Lybius dubius Bearded Barbet	8	4	179		1	2	1	
Lybius vielloti Vieillot's Barbet			57		10		7	

Picidae

Dendropicos fuscescens Cardinal Woodpecker			4	1	2	1
Mesopicos goertae Grey Woodpecker			1			

Pycnonotidae

Species	1	2	3	4	5	6	7	8
Pycnonotus barbatus Common Bulbul	51	46	62	11	10	48	52	16
Chlorocichla flavicollis Yellow-throated Leaflove	1	4	49					4
Turdidae								
Turdus pelios African Thrush	45	4	41	13		12	20	
Muscicapidae								
Myrmecocichla cinnamomeiventris Mocking Chat	11	1	6			23		
Melaenormis edolioides Northern Black Flycatcher	1	1						
Sylviidae								
Eremomela pusilla Senegal Eremomela	17	5	4			1	1	
Sylvietta brachyura Northern Crombec	1			1				1
Phylloscopus trochilus Willow Warbler		1	7					
Sylvia borin Garden Warbler	6					11		
S. communis Common Whitethroat	1	25	18	2		11	13	
Cisticolidae								
Camaroptera brachyura Grey-backed Camaroptera			5					

Species	C1	C2	C3	C4	C5	C6	C7
Prinia subflava Tawny-flanked Prinia		9				8	3

Platysteiridae

Species	C1	C2	C3	C4	C5	C6	C7
Batis senegalensis Senegal Batis							2

Monarchidae

Species	C1	C2	C3	C4	C5	C6	C7
Elminia longicauda Blue Flycatcher			1				
Terpsiphone viridis Paradise Flycatcher							3

Timaliidae

Species	C1	C2	C3	C4	C5	C6	C7
Turdoides plebejus Brown Babbler		13				1	

Remizidae

Species	C1	C2	C3	C4	C5	C6	C7
Anthoscopus parvulus Yellow Penduline Tit							1

Nectariniidae

Species	C1	C2	C3	C4	C5	C6	C7
Chalcomitra senegalensis Scarlet-chested Sunbird	4	1	27	3		15	
Nectarinia venusta Variable Sunbird			1	1			

Zosteropidae

Species	C1	C2	C3	C4	C5	C6	C7
Zosterops senegalensis Yellow White-eye		4	12	2	6	22	4

Sturnidae

Species	C1	C2	C3	C4	C5	C6	C7
Onychognathus morio Neumann's Starling	15		1				

Species							
Lamprotornis purpureus Purple Glossy Starling		183		1	40	61	
Cinnyricinclus leucogaster Violet-backed Starling		25					
Passeridae							
Passer griseus Grey-headed Sparrow							1
Ploceidae							
Ploceus heuglini Heuglin's Masked Weaver		1					
P. cucullatus Village Weaver	9		4			87	
Estrildidae							
Estrilda caerulescens Lavender Waxbill	31	24	1	9	3	1	
Lagonosticta sanguinodorsalis Rock Firefinch		1		1			
L. senegala Red-billed Firefinch							1

CHAPTER 3

The role of avian frugivores in the germination and dispersal of fleshy-fruited *Ficus*

species in KwaZulu-Natal, South Africa

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Running header: Role of avian frugivores in the germination of fleshy-fruited *Ficus* spp.

3.1 Abstract

Figs (*Ficus* spp.) are a diverse taxon of woody plants that play keystone ecological roles. They provide nutritional and aseasonal fruit crops that are consumed by many frugivores, often in times of fruit scarcity. In a mutually beneficial relationship, the plants also benefit from seed dispersal by birds and mammals away from the parent plants enhancing germination and plant recruitment. Here, we assessed the effect of ingestion of *Ficus* fruit by avian frugivores, compared with manually de-pulped fruit and whole fruits, on seedling emergence and cumulative germination of three *Ficus* spp. (*F. sur, F. lutea* and *F. natalensis*). Fruits of *Ficus* spp. were fed to Dark-capped Bulbuls *Pycnonotus tricolor*, Knysna Turacos *Tauraco corythaix*, Purple-crested Turaco *Gallirex porphyreolophus*, Red-winged Starlings *Onychognathus morio*, Speckled Mousebirds *Colius striatus* and invasive Rose-ringed Parakeets *Psittacula krameri*. We recorded seed retention time as the time from the ingestion of seeds to the first appearance when excreted by the birds. Seeds removed from excreta, manually de-pulped seeds, and whole fruit were planted concurrently in soil trays in a greenhouse. Seedling emergence was recorded daily, and the proportion of seed germinated was calculated as germination success. Germination success of avian ingested seeds increased significantly compared with seeds in whole fruit and manually de-pulped seeds, except seed germination for *F. sur* seeds ingested by Dark-capped Bulbuls. Ingested seeds germinated the fastest, followed by seeds in whole fruits and lastly, de-pulped seeds. *Ficus sur* and *F. lutea* ingested seeds had higher germination percentages than *F. natalensis*. Our results showed that ingestion by birds typically improved *Ficus* seed germination as well as the additional positive effects of seed movement. These findings have important implications with the potential to improve *Ficus* seed dispersal, promote regeneration and sustain populations of the many vertebrates that depend on fig fruit.

Keywords: Seed germination; Avian frugivores; *Ficus* species; Seed retention time; Keystone species.

3.2 Introduction

Fleshy fruited *Ficus* species have been recognised as one of the most important plant genera for tropical frugivores (Shanahan et al. 2001; Zhang et al. 2006; Heer et al. 2010; Cottee-Jones et al. 2013). They are regarded as keystone species because they exhibit extensive fruit production with an attractive fleshy pulp able to sustain avian frugivores throughout periods of food scarcity (Compton et al. 1996; Kalko et al. 1996; Korine et al. 2000; Righini et al. 2004; Zhang et al. 2006; Kirika et al. 2007; Compton and Greeff 2020). Fig fruits availability during periods of food scarcity often influences the entire community, especially serving as a dry season staple for frugivorous mammals and birds (Jeevanandam and Corlett 2013). The genus *Ficus* (figs; Moraceae) is one of the largest plant genera with more than 750 described species distributed worldwide, mainly in tropical countries (Jeevanandam and Corlett 2013). Fig trees occupy diverse habitats and attain a wide range of growth forms that include large woody climbers, hemi-epiphytes, as well as trees and shrubs. Globally over 1200 birds and mammals species feed on *Ficus* fruit (Sanahan et al. 2001; Kattan and Valenzuela 2013) and over 10% of the World's birds and 6% of mammals consume figs, making them one of the most widely consumed plant taxon.

Avian frugivores are important seed dispersers because of their ability to move within and between habitats. Birds commonly ingest the entire fruit and regurgitate or defecate the seeds, affecting the germination potential of the seeds (Yagihashi et al. 1998; Charalambidou et al. 2003; Samuels and Levey 2005; Jordaan et al. 2011; Wilson and Downs 2012; Mokotjomela et al. 2013). Ingested seeds can undergo mechanical and chemical scarification of the seed coat, thus enhancing the removal of germination inhibitors (D'Avila et al. 2010;

Fedriani et al. 2011; Czarnecka et al. 2012; Thabethe et al. 2015; Díaz Vélez et al. 2018). Seeds in excreta may have reduced risks of predation and or microbial attacks (Witmer and Cheke 1991; Moore 2001; Herrera 2003; Wilson and Downs 2012). The residue in the defecated seeds provides nutrients that enhance germination and promote seedling establishment (Traveset 1998; Figueroa and Castro 2002; Chimera and Drake 2010; D'Avila 2010; Fricke et al. 2013).

Although the effect of bird ingestion on seed germination has received considerable attention, results are not universal. This variance may be because of several factors such as seed size, seed coat structure, the number of seeds ingested, experimental conditions, and seed retention time (reviewed in Traveset 1998; Traveset et al. 2001; Chama et al. 2013).

Many studies have found that seeds ingested (regurgitated or defecated) by frugivores often have better germination success when compared with seeds not-ingested (Traveset 1998: Paulsen and Högstedt 2002; Jordaan et al. 2011; Fricke et al. 2013), while other studies have found decreased seed germination (LaRosa et al. 1985; Nogales et al. 2005) or that seed germination remains unaffected by gut passage (Wilson and Downs 2012). Various studies (Jordano 1983, 2000; Debussche and Isenmann 1994; Crawley 2000; Witkowski and Garner 2008; Francisco et al. 2008; Vaz Ferreira et al. 2011; Thabethe et al. 2015) have shown that some avian frugivores are seed predators or illegitimate seed dispersers because of their handling behaviour. Others have shown some plant species depend entirely on ingestion by frugivores for germination (Noble 1975; Wilson and Downs 2012).

Plants with fleshy fruits consist of nutritional fruit pulp surrounding their seeds, which serve as important sources of nutrition and energy for frugivorous animals worldwide (Herrera 1995; Jordano 2000; Gosper et al. 2005; Wilson and Downs 2011a). This mutually beneficial process between avian frugivores and fleshy fruited plants (Jordaan et al. 2011; Mokotjomela et al. 2013; Thabethe et al. 2015; Molefe et al. 2019) play an essential role in maintaining the

structure and diversity of many tropical ecosystems ranging from restoration to conservation of important keystone indigenous plant species (Jordano 2000; Shanahan et al. 2001; Kirika et al. 2008; Fedriani et al. 2011; Wilson and Downs 2012; David et al. 2015).

The importance of *Ficus* fruits in sustaining frugivorous species across many ecosystems (Shanahan et al. 2001; Zhang et al. 2006; Heer et al. 2010; Peabotuwage et al. 2019; Compton and Greeff 2020) suggests that the loss of *Ficus* plants might drive many dependent frugivorous animal species to extinction (Lambert and Marshall 1991; Kirika et al. 2007). Hence, investigating the role in which gut passage plays in the germination of *Ficus* spp. can assist in understanding ecosystem dynamics and conservation management.

In this study, we assessed the effects of six avian frugivores on the germination of three *Ficus* spp. (*F. sur, F. natalensis* and *F. lutea*) that belong to two subgenera; Sycomorus and Urostigma (Table 3.1). We compared the germination rate and success of avian ingested seeds and non-ingested (manually de-pulped seeds and whole fruit) by recording seedling emergence and analysing seed retention time and germination percentages. We predicted that fruit processing via avian gut passage would increase seedling emergence rate and germination success of ingested *Ficus* spp. compared with seeds from fruits with pulp removed and from whole fruits.

3.3 Materials and methods

3.3.1 Plant and bird species

Fresh, ripened *Ficus* fruit species used in the study (Table 3.1) were collected randomly from trees around Pietermaritzburg and Durban, KwaZulu-Natal Province, South Africa, 24 – 48 h before feeding trials. Bird species selected for this study have been previously observed feeding on *Ficus* spp. in the study area (Wilson and Downs 2012; Thabethe et al. 2015; pers. obs.). In order of increasing mean body mass, these were the native Dark-capped Bulbuls *Pycnonotus*

tricolor (± 38 g), Speckled Mousebirds *Colius striatus* (± 58 g), Red-winged Starlings *Onychognathus morio* (± 130g), Purple-crested Turacos *Gallirex porphyreolophus* (± 305g), and Knysna Turacos *Tauraco corythaix* (± 300g). We also studied the invasive Rose-ringed Parakeets *Psittacula krameri* (± 130g).

3.3.2 Capture and maintenance of study birds

We conducted this study at the Animal House, University of KwaZulu-Natal (UKZN), Pietermaritzburg, South Africa. Native bird species, including Dark-capped Bulbuls (n = 7), Red-winged Starlings (n = 5), Knysna Turacos (n = 3), Purple-crested Turacos (n = 3), and Speckled Mousebirds (n = 3), as well as the invasive exotic Rose-ringed Parakeets (n = 5) that had been in captivity for more than a year in outside aviaries, were used in our study. We caught the birds and moved them indoors to a constant environment room where they were caged (42.7 × 43 × 59.3 cm) individually. Clean removable plastic trays laid with newspaper were placed under each cage to facilitate the collection of individual excreta, and the removal of seeds from these. Birds were acclimatised in the constant environment room with 12L: 12D photoperiod at 25 ± 1 °C for a week before the experimental trials were conducted.

We fed birds a daily maintenance diet of mix fresh fruits including pears, apples, bananas, oranges and carrots, either grated or chopped. A mixture of AviPlus Softbill/ Mynah pellets and crumble (Avi-products, Durban, South Africa) were added to supplement the maintenance diets. Sunflower seeds (*Helianthus* spp.) were added to the diet of Rose-ringed Parakeets. Drinking water was provided at all times.

3.3.4 Feeding trials

The respective fresh *Ficus* spp. fruit were collected and was incorporated into the maintenance diet a day before experimental trials. On the experimental trial days, we fed birds with only the

respective *Ficus* spp. Fruits were weighed to 0.01g, and birds were weighed 30 min before the trials. Each *Ficus* fruit species was offered whole or cut to an individual bird once within a 12 h period. We observed birds from the beginning of the trials to observe the feeding behaviour of each bird individual.

3.3.5 Seed retention time (SRT)

We measured the seed retention time as the time from when the bird first ingested the experimental fruits to the time when seeds first appeared in the excreta. We collected seeds in excreta at the end of each experimental trial. We measured seed retention time on the experimental day only.

3.3.5 Germination trials

We removed seeds from the excreta of individual birds and planted them in separate trays (265 x 180 x 75 mm) containing potting soil with no additives within 24 h of the end of each feeding trial. We did not wash seeds before planting and were covered with a soil layer approximately 0.5 cm deep (Wilson and Downs, 2012; Thabethe et al., 2015). We planted whole fruits and manually de-pulped seeds as controls in the same manner as ingested seeds. All seed trays were housed in a greenhouse at UKZN and watered daily. We considered the seeds as germinated when seedlings first emerged through the soil surface. The number of germinated seeds were counted and recorded daily, and seedlings were removed from the tray after counting.

3.3.6 Data analyses

Cumulative germination was tested using a one-way analysis of variance (ANOVA) to compare germination success of seed ingested by specific avian frugivores species with seed from de-pulped and whole fruits control. Seedling emergence was calculated as the time of

sowing until the first seedling emergence. Seed retention time and seedling emergence were analysed using a non-parametric analysis; a Kruskal-Wallis test, because the data used were not normally distributed. Further investigations with post hoc Tukey tests were performed where significant differences were evident. All analyses were performed using R (version 3.6.1, R Core Team 2018) and Past (version 3.14, Hammer et al. 2001).

3.4 Results

3.4.1 Ficus spp. fruit ingestion

Speckled Mousebirds did not feed on the *Ficus* spp. fruits, so their respective trials were stopped after a few hours. All other birds species used in the study ingested the *Ficus* fruits (Fig. 3.1). The Dark-capped Bulbuls ingested the least of the three *Ficus* fruits (*F*. natalensis ~55 ± 4.6 g per day, *F.lutea* ~60 ± 9.4 g per day and *F. sur* ~45 ± 9 g per day) while the Red-winged Starlings ate the most (121 ± 15 g per day) for *F. sur* fruits, Knysna Turacos ingested the most for *F. natalensis* (125 ± 3.5 g per day) while Rose-ringed Parakeets the most (110 ± 12 g per day) for *F. lutea* (Fig. 3.1). There was a significant difference in the amount of *F. lutea* and *F. sur* fruit (g) ingested by Dark-capped Bulbuls and the other four birds species used in the study ($p < 0.05$; Fig. 3.1). There was a significant difference among the bird species in the mass of the fruit (g) of respective *Ficus* spp. eaten (*F. natalensis*, One-way ANOVA; $F_{4,19}$ = 69.43, $p < 0.0001$; *F. lutea,* ANOVA; $F_{4,19}$ = 10.66, $p < 0.0001$; *F. sur,* ANOVA; $F_{4,19}$ = 39.4, $p < 0.0001$; Fig. 3.1). The initial and final body masses of Dark-capped Bulbuls were significantly different when fed *F. lutea* (T-test; t =-3.33, df = 9, $p < 0.005$), *F. natalensis* (T-test; t = -2.44, df = 9, $p < 0.05$) and *F. sur* (T-test; t = -2.96, df = 9, $p < 0.05$, Fig. S3.1). However, there were no significant differences in the body masses of the other bird species before and after feeding on the respective *Ficus* spp. fruit (Supplementary Fig. S3.1).

The amount of fruit eaten per gram body mass (per g BM) varied significantly among five bird species fed *F. natalensis* (Kruskal-Wallis; $H_4 = 20.34$, $p < 0.005$), *F. lutea* (Kruskal-Wallis; $H_4 = 19.03$, $p < 0.001$), and *F. sur* (Kruskal-Wallis; $H_4 = 14.8$, $p < 0.005$; Fig. 3.2).
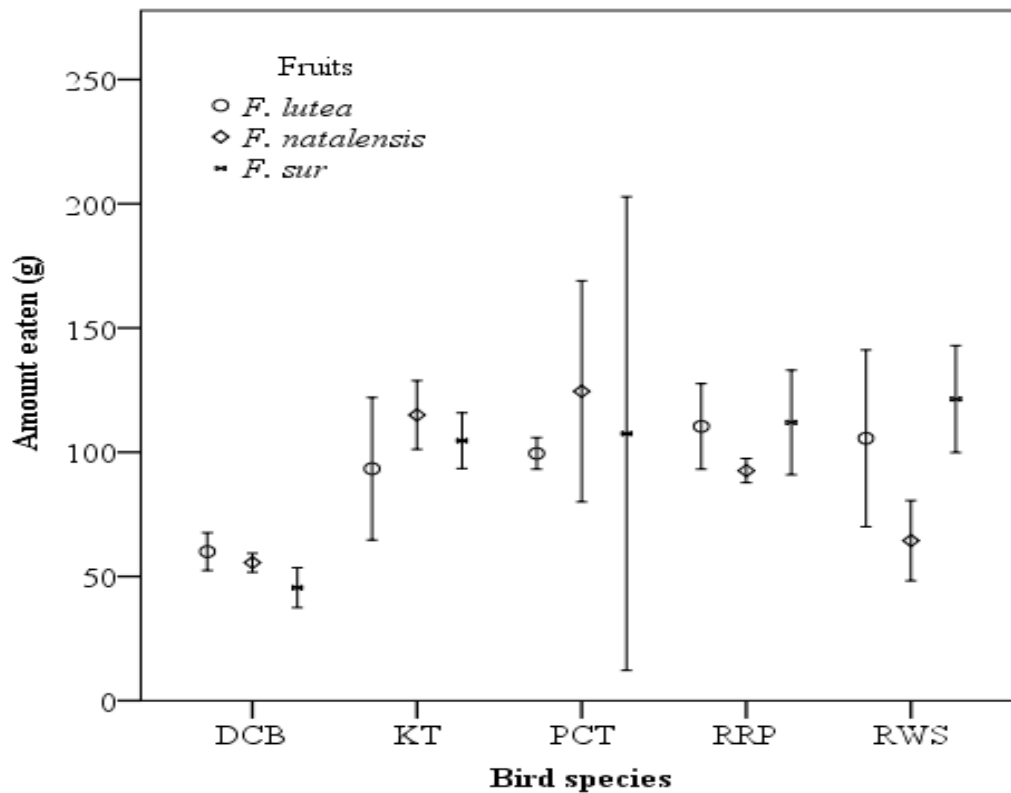
Fig. 3.1 The absolute mass (Mean ± SE) of *Ficus* spp. fruit eaten by four indigenous (Dark-capped bulbul-DCB, Red-winged Starling-RWS, Purple-crested Turaco-PCT and Knysna Turaco-KT) and one non-native (Rose-ringed Parakeet-RRP) frugivorous bird species
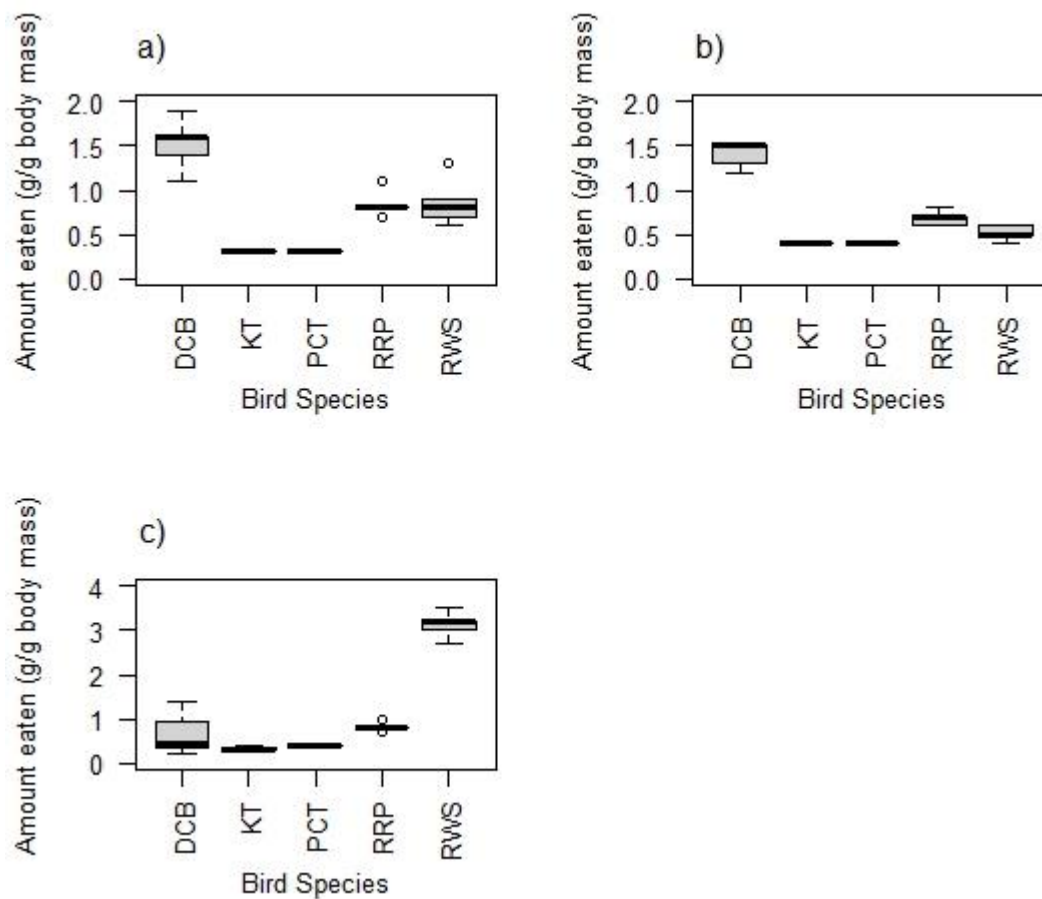
Fig. 3.2 The amount of the respective *Ficus* spp. fruit in terms of mass ingested per gram of the respective bird body masses where a) is *F. lutea*, b) is *F. natalensis*, and c) is *F. sur* fruits eaten by five avian species (Dark-capped bulbul-DCB, Red-winged Starling-RWS, Purple-crested Turaco-PCT and Knysna Turaco-KT, Rose-ringed Parakeet-RRP). (Note: Boxes are 25 and 75 % quartiles, the solid black squares within the boxes the medians, bars show 10 and 90 % values)

3.4.2 Seed retention time

Seed retention time (SRT) varied significantly among the avian species for *F. sur* seeds (Kruskal-Wallis; $H_3 = 9.81$, p = 0.02) and *F. lutea* (Kruskal-Wallis; $H_3 = 10.47$, p < 0.05). However, there was no significant difference in seed retention time among the avian species for *F. natalensis* (Kruskal-Wallis; $H_3 = 2.27$, p = 0.52, Tables 3.1 and 3.2). The Knysna Turaco had the shortest SRT (12.5 ± 3.5 min) when fed with *F. lutea*. Red-winged Starlings had the longest SRT (26.2 ± 13.5 min) when fed with *F. lutea*, and *F. sur* (30.8 ± 17.3 min) but the shortest SRT (15.0 ± 5.2 min) when fed with *F. natalensis*. Purple-crested Turacos had the longest SRT (20.7 ± 5.1 min) when fed with *F. natalensis* and shortest SRT (18.3 ± 6.5 min) when fed with *F. sur* (Table 3.2). *Ficus* fruits ingested by Rose-ringed parakeets were not excreted nor regurgitated within the period of observation. This could be, because, the fruits were first crushed with their phalanges before eating.

Table 3. 1 Characteristics of the three *Ficus* species used in the present study and seed retention time (Mean ± SD) measured in minutes of the respective seeds ingested by the avian frugivore species

Species	Fruiting period	Fruit colour when ripe	Fruit size (mm diameter)	Seed retention time (Mean ± SD)			
				Dark-capped Bulbul	Red-winged Starling	Purple-crested Turaco	Knysna Turaco
Ficus sur	All year	Orange-red	20-40	25.0 ± 8.9	30.8 ± 17.3	18.3 ± 6.5	24.0 ± 5.7
Ficus natalensis	All year	Reddish-brown	10-20	18.0 ± 7.0	15.0 ± 5.2	20.7 ± 5.1	16.0 ± 5.7
Ficus lutea	May-October	Yellowish-brown	15-30	23.2 ± 7.1	26.2 ± 13.5	19.0 ± 3.6	12.5 ± 3.5

Table 3.2 Dark-capped Bulbuls, Red-winged Starlings, Knysna and Purple-crested Turacos differences in seed retention time and mean time seedling emergence of *Ficus* species

Ficus Species	Seed retention time		Significance	Mean time to first seedling emergence		Significance
	H_2	*P*		H_2	*P*	
Ficus sur	9.8	<0.05	S	17.7	<0.05	S
Ficus natalensis	2.2	0.5	NS	3.3	0.3	NS
Ficus lutea	10	<0.05	S	1.4	0.7	NS

*Significant at $P < 0.05$; NS, not significant; S, significant

3.4.3 Mean seedling emergence time

The mean seedling emergence time of ingested seeds varied significantly among the avian species for *F. sur* (Kruskal-Wallis; $H_3 = 17.69$, $p < 0.005$) but not for *F. natalensis and F. lutea* (Table 3.2). *Ficus sur* and *F. lutea* seeds emerged sooner than *F. natal*ensis seeds (Fig. 3.3a,c, Table 3.2). Seeds ingested by Dark-capped Bulbuls emerged faster for *F. lutea* and *F. natalensis* than *F. sur* (Fig. 3.3a,b). Seeds ingested by the two species of Turaco emerged faster for *F. natalensis* and *F. sur* than *F. lutea* (Fig. 3.3b,c). Seeds ingested by avian frugivores emerged significantly sooner than whole and de-pulped seeds (Fig. 3.3) for the three *Ficus* spp.

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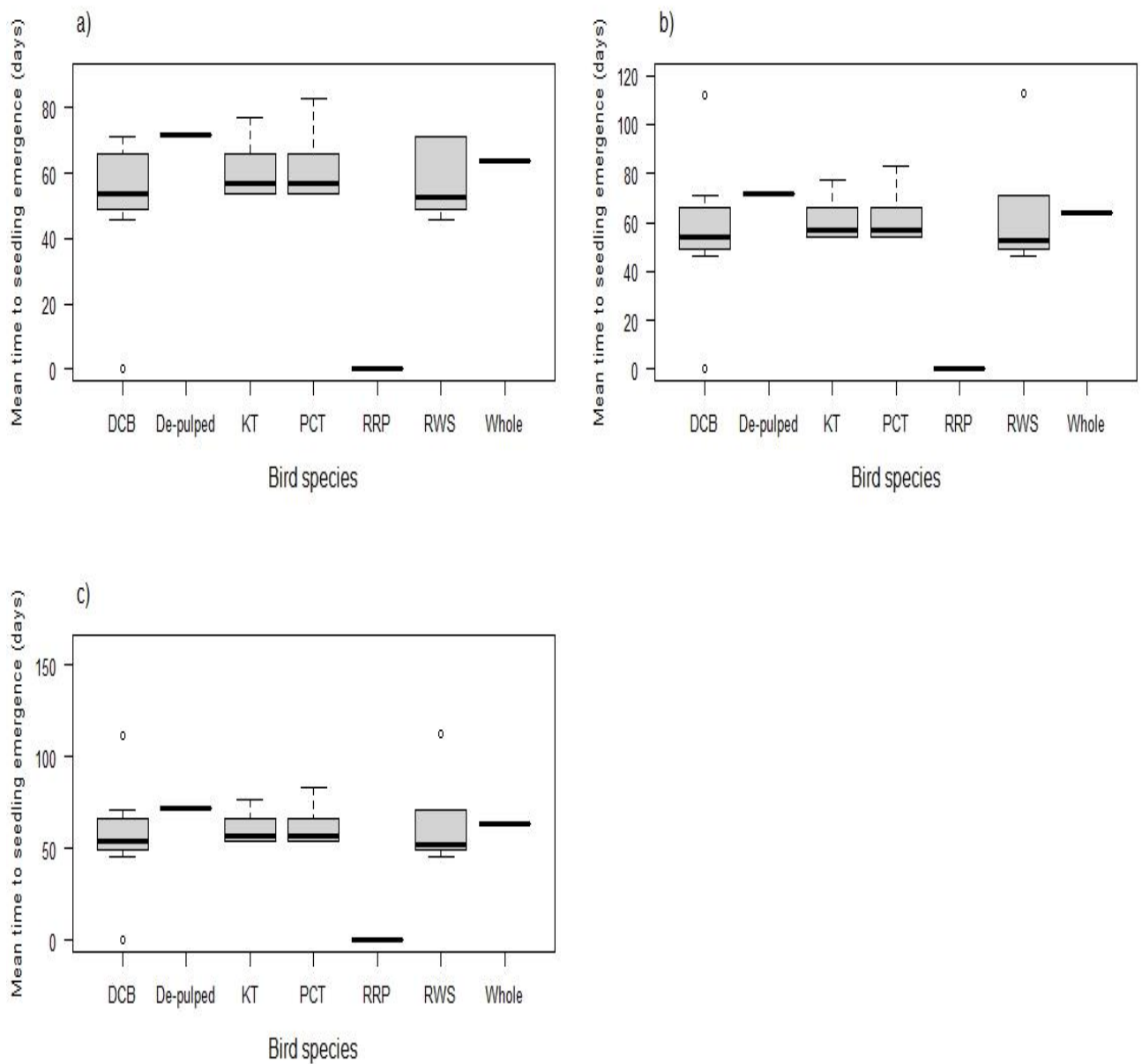
Fig. 3.3 Mean time to first seedling emergence of seeds ingested by avian frugivores (Dark-capped bulbul-DCB, Red-winged Starling-RWS, Purple-crested Turaco-PCT and Knysna Turaco-KT, Rose-ringed Parakeet-RRP, Depulped and Whole Fruits) for a) *F. lutea*, b) *F. natalensis*, and c) *F. sur.* (Boxes are 25 and 75% quartiles, the lines within the boxes indicate the medians, bars show 10 and 90% values, and dots highlight outliers).

3.4.4 Seedling germination success

The avian frugivores varied significantly in their effects on the cumulative germination of ingested seeds for the three *Ficus* spp. (Kruskal-Wallis; $H_5 = 274.7$, $p < 0.01$). Seeds ingested by Knysna and Purple-crested Turacos had higher cumulative germination than those ingested by Red-winged Starlings and Dark-capped Bulbuls for all *Ficus* spp. used in the study (Fig. 3.4). Cumulative germination of seeds ingested by the avian frugivores was significantly different to both whole and de-pulped seed for all the *Ficus* spp., except for *F. sur* ingested by Dark-capped Bulbuls (ANOVA; $F = 2.6$, $p = 0.9$ and $F = 0.02$, $p = 0.9$ respectively, Table 3.3). Cumulative germination of seeds from whole fruits was higher than de-pulped fruit for all *Ficus* species. Germination of seeds varied significantly between whole and de-pulped fruits among all species. Furthermore, *F. sur* had the highest mean cumulative germination and germinated sooner than *F. lutea* and *F. natalensis.*
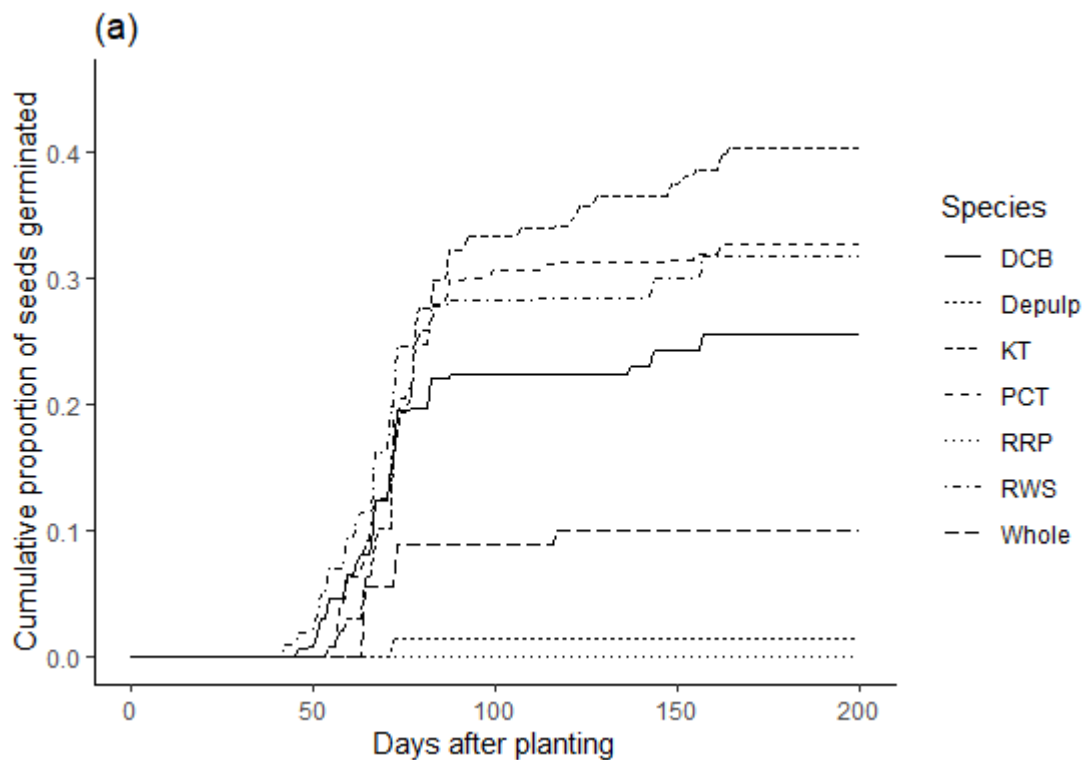
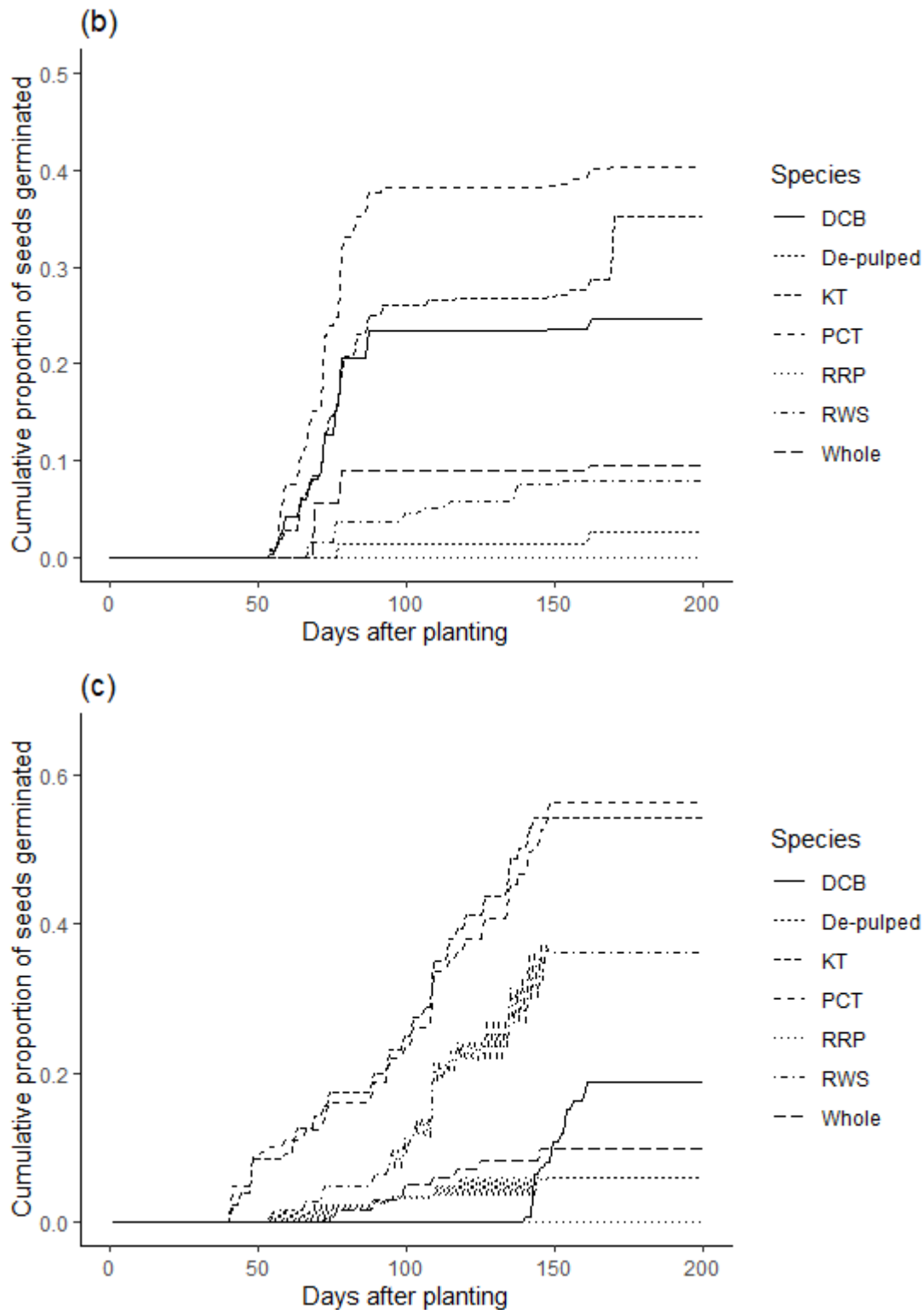**Fig. 3.4** Cumulative germination of seeds ingested by four avian frugivores (Dark-capped bulbul-DCB, Red-winged Starling-RWS, Purple-crested Turaco-PCT and Knysna Turaco-KT, Rose-ringed Parakeet-RRP), whole and de-pulped fruits for (a) *F. lutea*, (b) *F. natalensis*, and (c) *F. sur* in the present study

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Table 3. 3 Differences between cumulative germination of avian ingested seeds compared with de-pulped seeds and whole fruits respectively for the three *Ficus* species (NS not significant; S significant)

Ficus Species	Avian frugivores	Cumulative germination of seeds from					
		De-pulped fruit compared with ingested seeds			Whole fruit seeds compared with ingested seeds		
		F_1	*P*		F_1	*P*	
Ficus natalensis	Dark capped Bulbul	271.4	<0.01	S	104	<0.001	S
	Red-winged Starling	119.2	<0.01	S	21.43	<0.01	S
	Knysna Turaco	258.4	<0.01	S	118.2	<0.01	S
	Purple-crested Turaco	292.7	<0.01	S	177.8	<0.01	S
Ficus sur	Dark capped Bulbul	0.02	0.9	NS	2.6	0.9	NS
	Red-winged Starling	57.95	<0.01	S	43.14	<0.01	S
	Knysna Turaco	135.7	<0.01	S	120.6	<0.01	S
	Purple-crested Turaco	138.7	<0.01	S	122.1	<0.01	S
Ficus lutea	Dark capped Bulbul	228.8	<0.01	S	75.43	<0.01	S
	Red-winged Starling	246.4	<0.01	S	110.6	<0.01	S
	Knysna Turaco	204.2	<0.01	S	107.7	<0.01	S
	Purple-crested Turaco	222.3	<0.01	S	106.1	<0.01	S

3.5 Discussion

In this study, we found all the bird species except for Speckled Mousebirds ingested the respective *Ficus* spp. fruit. Germination rates of *Ficus* seeds ingested by avian frugivores in the study were significantly improved compared with de-pulped and whole fruit. The amount of *Ficus* fruit ingested by birds varied, with Dark-capped Bulbuls (the smallest avian species) consuming the least. This is consistent with other studies that found that smaller birds consumed fewer seeds than larger birds (Molefe et al. 2019; Dlamini et al. 2018). A previous

study suggested that the amount of fruit consumed by each avian species is not necessarily related to the amount of seed excreted (Dlamini et al. 2018). However, there was a correlation in the amount of fruit consumed and seed excreted by birds in our study, except for Rose-ringed Parakeets that ate the most for *F. lutea* but did not excrete viable seeds. This may be attributed to their handling and feeding behaviour, considering that they are seed predators (Jordano 1983; Janzen 1971; Thabethe et al. 2015). Although, some studies also considered them as illegitimate seed dispersers, in cases where few fruits were regurgitated and managed to germinate or when they moved fruits away from the mother plant and dropped on fertile ground to grow (Moles et al. 2003; Guerrero and Tye 2009; Young et al. 2012). Avian ingestion effects on germination have often been attributed to several factors, including physiological and morphological traits associated with both plant and avian species (Barnea et al. 1991; Voigt et al. 2011; Wilson and Downs 2012; Thabethe et al. 2015).

The SRT obtained in this study was approximately between ~12.5 - 30.8 min, indicating that transit times were long enough to enhance seed germination and allow dispersal of *Ficus* fruits away from their parent plant. There has been conflicting evidence on the effects of long versus short seed retention time (SRT) on seed germination rates. Our study showed that seed retention time ranges from (Fastest SRT, 12.5 ± 3.5 min) for *Ficus lutea* ingested by Knysna Turaco and (slowest SRT, 30.8 ± 17.3 min) for *Ficus sur* consumed by Red-winged Starlings which is similar to the findings by Wilson and Downs (2012). A previous study showed that long SRT had higher rates of seed germination (Barnea et al. 1991), while other studies found a decrease in seed germination rate (Murray et al. 1994; Charalambidou et al. 2003), and some, no impact (Barnea et al. 1990; Jordaan et al. 2011; Dlamini et al. 2018; Molefe et al. 2019). In the latter cases, the avian frugivores primary function was to disperse seeds (Jordaan et al. 2011; Molefe et al. 2019). However, longer SRT may be of benefit to plant in terms of longer dispersal distance, germination, and plant fitness (Fukui 2003; Wilson and Downs 2012).

Ingestion by birds has been suggested to affect seed germination (Robertson et al. 2006; Wilson and Downs 2012; Thabethe et al. 2015) and dispersal, either by increasing or decreasing germination success (Traveset 1998; Wilson and Downs 2012). Consistent with other studies (Barnea et al. 1991; Voigt et al. 2011; Jordan et al. 2012; Dlamini et al. 2018), our results showed that frugivore gut passage had a positive effect on seedling emergence and germination success. De-pulped and whole fruits for all *Ficus* species germinated later than ingested seeds.

Contrary to several studies that reported de-pulped seeds to emerge sooner than whole fruits seedlings (Barnea et al. 1991; Panetta and McKee 1997; Meyer and Witmer 1998; Day et al. 2003; Panetta 2001; Jordano et al. 2011; Thabethe et al. 2015). Our results showed that whole fruit germinated sooner than de-pulped, suggesting that manual pulp removal might not necessarily improve germination as found in some other studies, but rather seed germination was improved by seed coat abrasion and dispersal by avian species gut passage (D'Avila et al. 2010; Wilson and Downs 2012).

Although Speckled-Mousebirds did not ingest seeds during the experimental trials, they were observed feeding and handling *Ficus* species in the wild (pers. obs.). It would therefore be interesting to see how effective they are as seed dispersers in the wild.

Consistent with previous studies, we found that avian ingestion plays a vital role in the germination success and potential seed dispersal of the respective fleshy fruited *Ficus* spp. With the potential to improve fig seed dispersal, germination success and emergence of the keystone *Ficus* spp., they promote regeneration. This relationship is important for *Ficus* fruit and the populations of many vertebrate species that depend on them, especially in times of other fruit scarcity.

3.6 Acknowledgements

3.7 References

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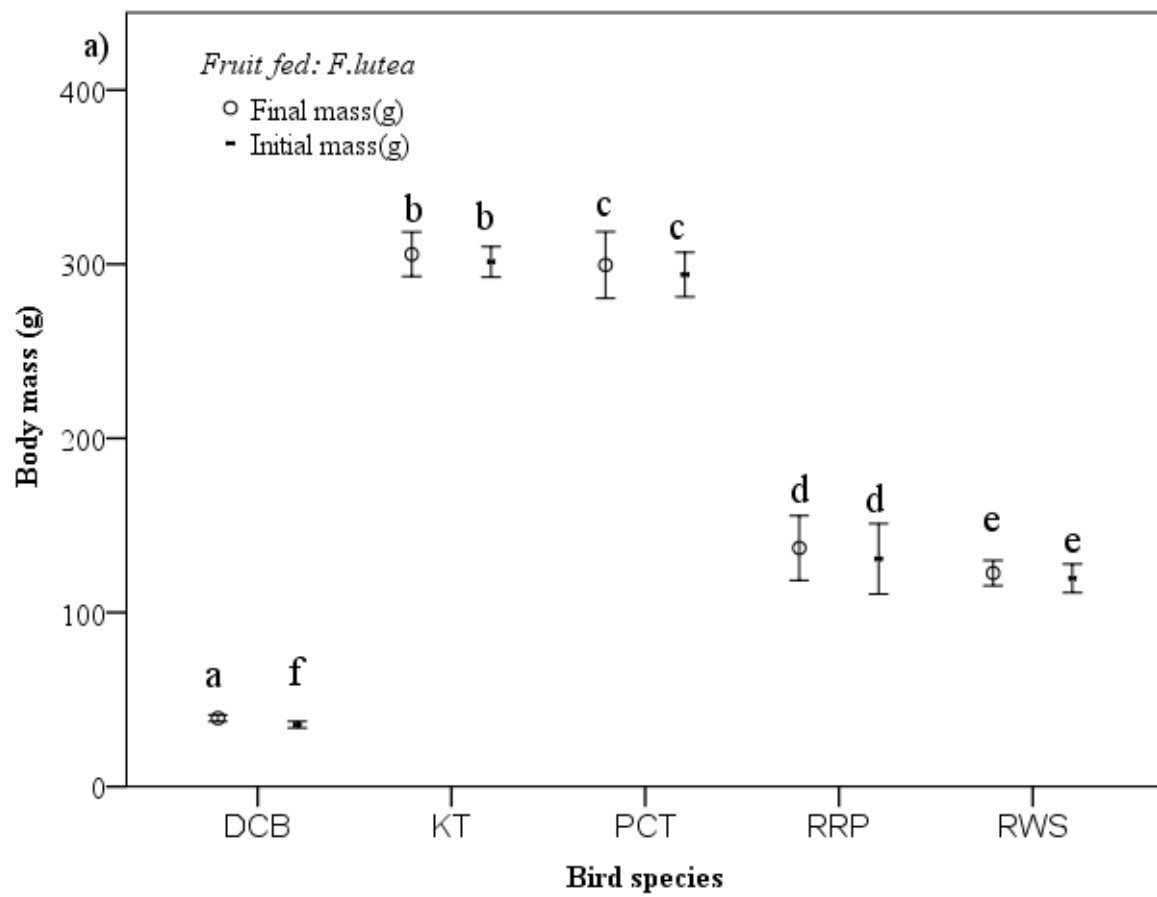Jordano P (2000) Seeds: The Ecology of Regeneration in Plant Communities. CAB International, Wallingford, UK, 125–166

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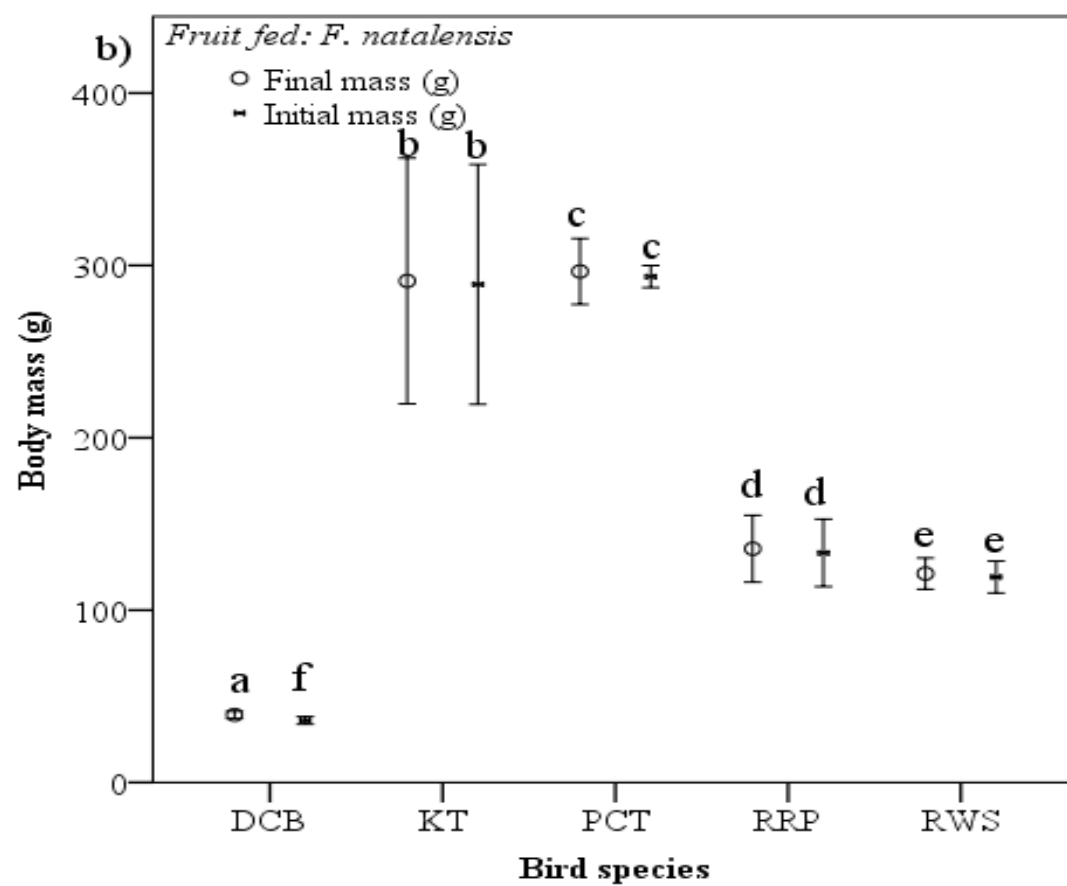
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3.8 Supplementary information

b)

Fruit fed: F. natalensis

- ○ Final mass (g)
- Initial mass (g)
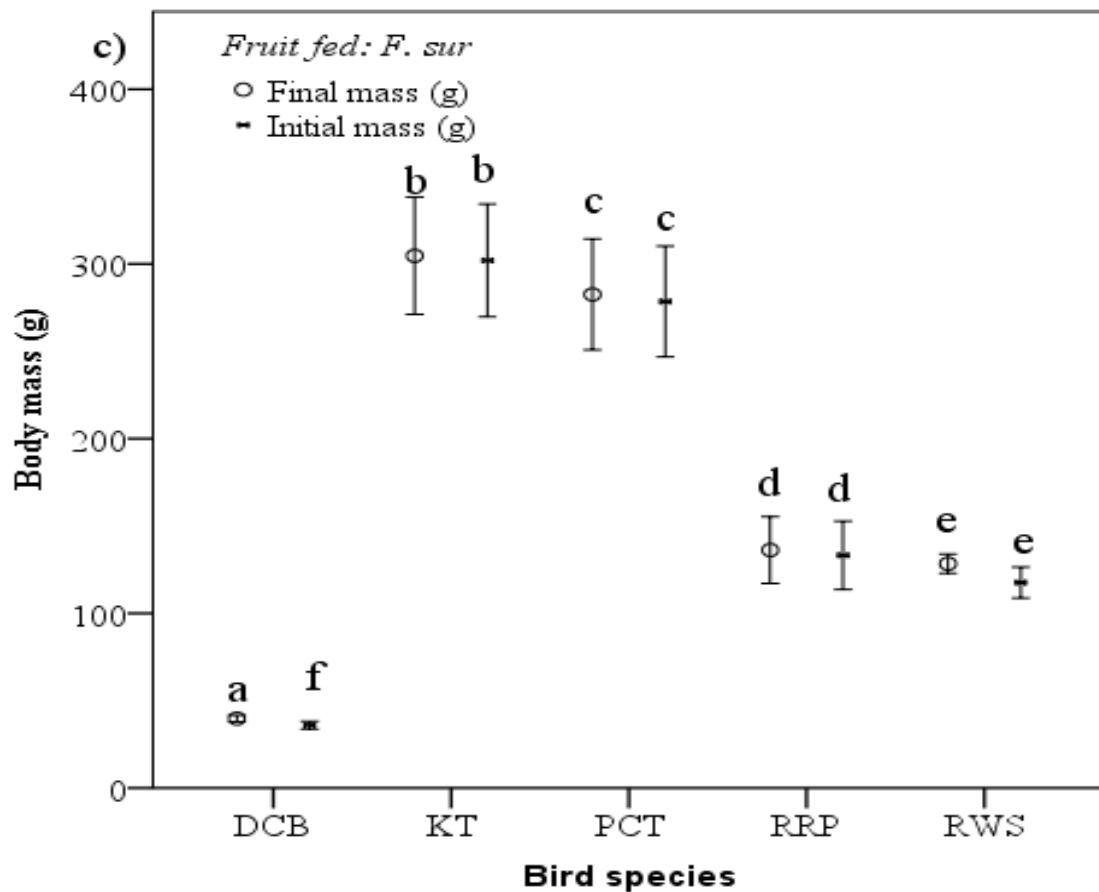
Supplementary Fig. S3.1 The final and initial mean (± SE) body masses of four indigenous (Dark-capped bulbul-DCB, Red-winged Starling-RWS, Purple-crested Turaco-PCT and Knysna Turaco-KT) and one non-native (Rose-ringed Parakeet-RRP) frugivores bird species, fed fruit a) *F. lutea*, b) *F. natalensis* and c) *F. sur*. (Treatments with letters in common were not significantly different ($p < 0.05$).

CHAPTER 4

Does *Ficus* species seed ingestion by Wahlberg's epauletted fruit bats enhance germination and seedling emergence?

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Running header: Fruit bats enhance germination and seedling emergence of *Ficus* species

4.1 Abstract

Ficus species are keystone species for many frugivorous species. Passage of seed through frugivorous bats gastrointestinal system potentially influences seed dispersal, germination and seedling emergence. We investigated the effects of Wahlberg's epauletted fruit bats, *Epomophorus wahlbergi*, ingestion and gut passage on germination and seedling emergence of various *Ficus* species. We predicted that the fruit bats would positively influence the germination of *Ficus* species used in the study. We fed fruit bats fruits of four *Ficus* species, *F. sur*, *F. tricopoda*, *F. lutea* and *F. sycomorus* collected around Pietermaritzburg and Durban, KwaZulu-Natal Province, South Africa, in separate laboratory feeding trials. Germination amounts were relatively high for all ingested seeds. Our results showed that the germination of *Ficus* seeds was positively influenced by passage through the gut of *E. wahlbergi*. Whole fruit had significantly less germination success than spat seeds and de-pulped seeds for all *Ficus* species used in the study, except *F. lutea*; they mostly germinated at approximately the same time but had a higher germination success. We found *E. wahlbergi* consumed proportionally significant amounts of the *Ficus* fruits. We observed *E. wahlbergi* feeding and spreading the seeds of figs away from the mother plant in the wild. They usually carried the fruits away to feeding roosts where seeds were dropped, thereby dispersing seeds and fruits. Based on our results, *E. wahlbergi* are important in seed dispersal and germination of keystone *Ficus* species.

Key words: *Epomophorus wahlbergi*, *Ficus*, seed emergence, germination success, gut passage

4.2 Introduction

Fruit-frugivore interactions are mutually beneficial, providing several functional services to ecological processes. These include but are not limited to transportation of seeds away from parent plants (seed dispersal), forest regeneration and biodiversity maintenance (Fenner & Thompson; 2005; Jordaan *et al*. 2011; Kitamura 2011; Helbig-Bonitz 2013; Caughlin *et al*. 2013; Sasal *et al*. 2013; Shikang *et al*. 2015). These interactions may also increase or decrease germination probability after seeds have passed through frugivore's guts and reduce seed germination time (i.e. seedling emergence) after consumption (Traveset & Verdú 2002; Samuels & Levey 2005; Pires *et al*. 2018).

Seed germination is one of the most important stages of the seed dispersal cycle necessary for the first stage of plant establishment (Wang & Smith 2002; Traveset *et al*. 2007; Tang *et al*. 2007; Jordaan *et al*. 2012; Mokotjomela *et al*. 2013; Traveset *et al*. 2014; Thabethe *et al*. 2015; Saldaña-Vázquez *et al*. 2019; Molefe *et al*. 2020; Stringer *et al*. 2020). This includes fruit pulp removal, passage through the gut in the case of small-seeded fruits (Traveset 1998; Traveset & Verdú 2002; McConkey & Drake 2006; Saldaña-Vázquez *et al*. 2019), the duration of this passage, the chemical and mechanical conditions within the digestive tract (Traveset *et al*. 2007), as well as the composition and number of defecated seeds (Samuels & Levey 2005; Robertson *et al*. 2006). Although not all seed dispersers assist seed germination equally, however, fruit bats are one of the frugivores that are important seed dispersers for many plant species (Traveset 1998; Traveset & Verdú 2002; McConkey & Drake 2006; Saldaña-Vázquez *et al*. 2019).

Fruit bats are recognised as important species in preserving and restoring natural flora in tropical regions (Fujita & Tuttle 1991; Lobova *et al*. 2009). Fruit bats role in seed germination function, dispersal of seeds and pollination is essential and crucial in the succession and composition of plant communities (Henry & Jouard 2007; Muscarella &

Fleming 2007). Fruit bats can travel relatively large distances (Webb & Tidemann 1996; Bernard & Fenton 2002; Richter & Cumming 2006; Heer *et al*. 2010; Rollinson *et al*. 2013; Pulzatto *et al*. 2018), often with fast and direct flight patterns (Tsoar *et al*. 2011), and crossing open expanses in fragmented landscapes (Muscarella & Fleming 2007; Seltzer *et al*. 2013; Baker *et al*. 2018). Consequently, they are regarded as highly efficient dispersers of seeds to isolated and degraded areas (Cox *et al*. 1991; Muscarella & Fleming 2007; Schmelitschek *et al*. 2009; Pulzatto *et al*. 2018), so maintaining ecosystems, especially forests (Fleming & Heithaus 1981; Whittaker & Jones 1994; Muscarella & Fleming 2007; Jordaan *et al*. 2012). They provide important ecosystem services (Redford *et al*. 2013; Baker *et al*. 2018; van Toor *et al*. 2019; Laurindo *et al*. 2020) for enhancing restoration in disturbed habitats (Sritongchuay *et al*. 2014; Oleksy *et al*. 2015; Aziz *et al*. 2021). However, despite this evidence, there is still a paucity of fruit bat studies of seed dispersal, especially seed germination enhancement, a crucial factor in seed dispersal loop (Jordaan *et al*. 2012; Seltzer *et al*., 2013). More comprehensive and detailed studies are still needed (Jordaan *et al*. 2012; Aziz *et al*. 2021).

Fruit bats typically influence germination through their seed-handling behaviour (Djossa *et al*. 2008). They are also dietary specialists and have evolved to obtain their primary nutrients from fruits. Therefore, their fruit and seed handling behaviour may contribute to seed germination (Fleming 1986; Dumont 1999; Schupp *et al*. 2010; Rojas *et al*. 2011; Rojas *et al*. 2015; Saldaña-Vázquez *et al*. 2019). Reviews about the effect of seed passage through frugivore digestive tracts (guts) found that fruit bats enhanced seed germination compared with controls (Traveset & Verdú 2002; Saldaña-Vázquez *et al*. 2019). It was suggested that seed passage through fruit bats digestive tracts had physical and chemical effects on seed germination probability because they may alter the seed coat or endocarp (Traveset & Verdú 2002; Saldaña-Vázquez *et al*. 2019). Gut passage effects on seed germination have been

reported for some bird and fruit bat species (Robertson *et al*. 2006; Jordaan *et al*. 2012; Wilson & Downs 2012; Fricke *et al*. 2013; Thabethe *et al*. 2015; Stringer *et al*. 2020).

Fruit-eating bats may eat either whole fruits or parts of them; in the case of whole fruits, seeds pass through their digestive tract and can be found in faeces (Fleming 1981; Tang *et al*. 2007; Heer *et al*. 2010; Jordaan *et al*. 2012). The timing of the appearance of seeds in the faeces depends on the time of fruit ingestion and the gut transit time (Jordano *et al*. 2011; Downs *et al*. 2015). Wahlberg's epauletted fruit bat *Epomophorus wahlbergi* often pick fruit and fly to a feeding roost where they chew and squeeze the fruit between their tongues and palette ridges to extract the juice (Monadjem *et al*. 2010; Mqokeli & Downs 2013; Bonaccorso *et al*. 2014). Mouthfuls of seeds, exocarp and pulp fibre are then spat out (termed spats). Some fruit bats may only take a bite, ingest the fruit pulp, and reject masticated pellets. Fig eating fruit bats, for example, masticate figs and spit out spats with seeds (Morrison 1978; Charles-Dominique 1991; Izhaki *et al*. 1985; Tang 2007; Heer *et al*. 2010).

Figs (*Ficus*) species are important food resources for frugivores throughout the tropics (Izhaki *et al*. 1995; Shanahan *et al*. 2001; Heer *et al*. 2010; Wilson & Downs 2011; Pulzatto *et al*. 2018). Moreover, fruits of *Ficus* species are commonly consumed by fruit bats and dominate the diets of pteropodid fruit bats, with about 114 *Ficus* species consumed (Fujita & Tuttle 1991; Shanahan *et al*. 2001; Stier & Mildenstein 2005; Oleksy *et al*. 2015; Aziz *et al*. 2017, 2021). Furthermore, in a review, Aziz *et al*. (2021) reported *Ficus* to be the genera with the most bat-dispersed species (~60 species).

Fruits of fig trees are important resources for many frugivores, including fruit bat species, which also disperse the seeds (Shanahan *et al*. 2001; Monadjem *et al*. 2010; Bonaccorso *et al*. 2014). Therefore, we investigated the effect of *E. wahlbergi* ingestion and gut passage on the germination of several fleshy fruited *Ficus* species in this study. We

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predicted that fruit processing by *E. wahlbergi* would enhance the rapid germination of *Ficus* spp. seeds.

Table 4.1 Characteristics of the *Ficus* species used in the present study

Genus-Ficus Subgenus	Species	Fruiting period	Fruit size (mm diameter)	Fruit colour when ripe
Sycomorus	*Ficus sur*	All year	20-40	Orange-red
Sycomorus	*Ficus sycomorus*	All year	20-50	Yellowish-red
Urostigma	*Ficus lutea*	May-October	15-30	Yellowish-brown
Urostigma	*Ficus tricopoda*	May-January	15-35	Greenish-red

Data from Burrows & Burrows (2003), Griffiths & Lawes (2006), Boon (2010), Wilson & Downs (2012), and Raji & Downs (in prep.)

4.3 Methods

4.3.1 Study plant species

Ficus (figs; Moraceae) is one of the largest plant genera, disputably in lowland tropical rainforest with more than 850 described species distributed worldwide, mainly in tropical countries (Jeevanandam & Corlett 2013; Mabberley 2017; Mohapatra *et al*. 2020). Fig trees occupy diverse habitats and attain a wide range of growth forms that include large woody climbers, hemi-epiphytes, as well as trees and shrubs. Over 1200 animal species globally feed on *Ficus* (Cottee-Jones *et al*. 2016; Corlett 2017), and over 10% of the world's birds and 6% of mammals consume figs, making them the most widely consumed plant genus. Thus, *Ficus* species are a key component of fruit resources in tropical forests, sustaining numerous

frugivores and providing food resources during seasons of food scarcity. This attribute influences the entire community, usually by affecting the amount of available food serving as a dry season staple for birds, bats and other mammals (Jeevanandam & Corlett 2013; Makau 2016; Walther *et al*. 2018). Ripened and fresh *Ficus* fruit species used in the study (Table 4.1) were collected randomly from trees around Pietermaritzburg and Durban, KwaZulu-Natal Province, South Africa, within 24 – 48 h before feeding trials.

4.3.2 Study animal

Wahlberg's epauletted fruit bat *E. wahlbergi* is a relatively large (~100 -140 g) and common old World fruit bat (Monadjem *et al*. 2010). They occur widely in Africa, including along southern Africa's east coast (Monadjem *et al*. 2010). These bats are found in savannah, woodland and forest margins where fleshy fruits are available and occur in peri-urban areas (Heer *et al*. 2010; Jordaan *et al*. 2012; Rollinson *et al*. 2013, 2014; Downs *et al*. 2015; Downs *et al*. 2021). They forage for fleshy fruits and nectar during the night (Izhaki *et al*. 1995; Heer *et al*. 2010; Rollinson *et al*. 2013; Downs *et al*. 2015; Pulzatto *et al*. 2018). Individuals generally roost in dense, leafy trees or under the eaves of buildings (Fenton *et al*. 1985; Skinner & Chimimba 2005; Rollinson *et al*. 2013, 2014; Downs *et al*. 2015). Our study was conducted at the Animal House of the University of KwaZulu-Natal (UKZN), South Africa. We captured *E. wahlbergi* (n = 5) used in the feeding trials with mist-nets near UKZN (29°37'09.0"S 30°24'02.5"E; 29°37'12.1"S 30°25'03.7"E) under permit OP 25/2020 from Ezemvelo KZN Wildlife.

4.3.3 Feeding trials

Fruit bats were housed individually in cages (75×51×80cm) in a constant environment room set at 25 °C with a 12L: 12D photoperiod. They were acclimated for a minimum of 3 days before the experiment, with two days gap between consecutive feeding trials of the fruit species. During these times, fruit bats were fed a maintenance diet of papayas, pears, apples, and bananas supplemented with Aviplus softbill and crumble (Avi-products, Durban, South Africa) each evening a 20% sugar solution and water ad libitum.

We incorporated trial fruit into maintenance diets the day before the experiment. Ripe fruits of each *Ficus* species were offered to the fruit bats, within 48 h of picking, for 12 h (18:00–06:00) on the experiment day. The fruit was weighed before trials and presented whole or diced in feeding trays. Fruit bats were also each weighed before and after feeding. Control fruit were placed in the same room and weighed before and after trials. We covered clean plastic trays with newspaper and placed these under each cage to facilitate the removal of faeces and spats. Upon trial termination, dropped fruit and faeces were collected, and the total amount of uneaten fruit was weighed.

4.3.4 Germination trials

Seeds collected following bat-gut processing (seed ingested) were referred to as 'spat and faecal seed'. All spat and faecal seeds for each *Ficus* species from each *E. wahlbergi* were collected and planted within 24 h of the end of each feeding trial. We used separate soil trays (265 x 180 x 75 mm) containing potting soil approximately 0.5 cm deep with no additives for planting and placed these in a UKZN Botanical Garden greenhouse and watered them daily. Concurrently we manually depulped *Ficus* fruits, and planted these and whole fruits of each species in separate soil trays as controls, with no additives. Daily, we conducted germination

counts and removed the counted seedlings before watering. We observed trays until there was no further germination after a minimum of 120 days.

4.3.5 Data analyses

We compared the daily food intake (DFI) per gram body mass (g^{-1}mb) by *E. wahlbergi* for the various *Ficus* fruit species using a one-way analysis of variance (ANOVA). *Post-hoc* turkey tests were used for further investigation, where significant differences were evident. The mean cumulative proportion of seeds germinated was calculated for fruit bat ingested, de-pulped, and whole fruit seeds for each *Ficus* fruit species. Then, we compared these using a one-way analysis of variance (ANOVA). Finally, we compared the duration from planting until first germination (seedling emergence) for each *Ficus* fruit species between ingested seeds, de-pulped and whole fruit controls, with a Mann–Whitney U Test. We conducted all analyses using R (version 3.6.1, R Core Team 2018), Past (version 3.14, Hammer *et al*. 2001), STATISTICA 7 (Statsoft, Tulsa, USA) and PASW Statistics 18 (SPSS, Chicago, USA).

4.4 Results

4.4.1 *Ficus* fruit ingestion

Wahlberg's epauletted fruit bats consumed more *F. sur* (mean ± SE, 58.2 ± 5.7 g) compared with other *Ficus* species fruits fed. In addition, they ate significantly different amounts of the four *Ficus* fruit species presented in the study ($F_{3,16} = 7.395$; $P < 0.050$, Fig. 4.1). There was also a significant difference in the daily food intake of *Ficus* species by fruit bat relative to their body mass (DFI) ($F_{3,16} = 8.234$; $P < 0.050$, Fig. 4.1), consuming more than 50% of their body mass in fig fruits.
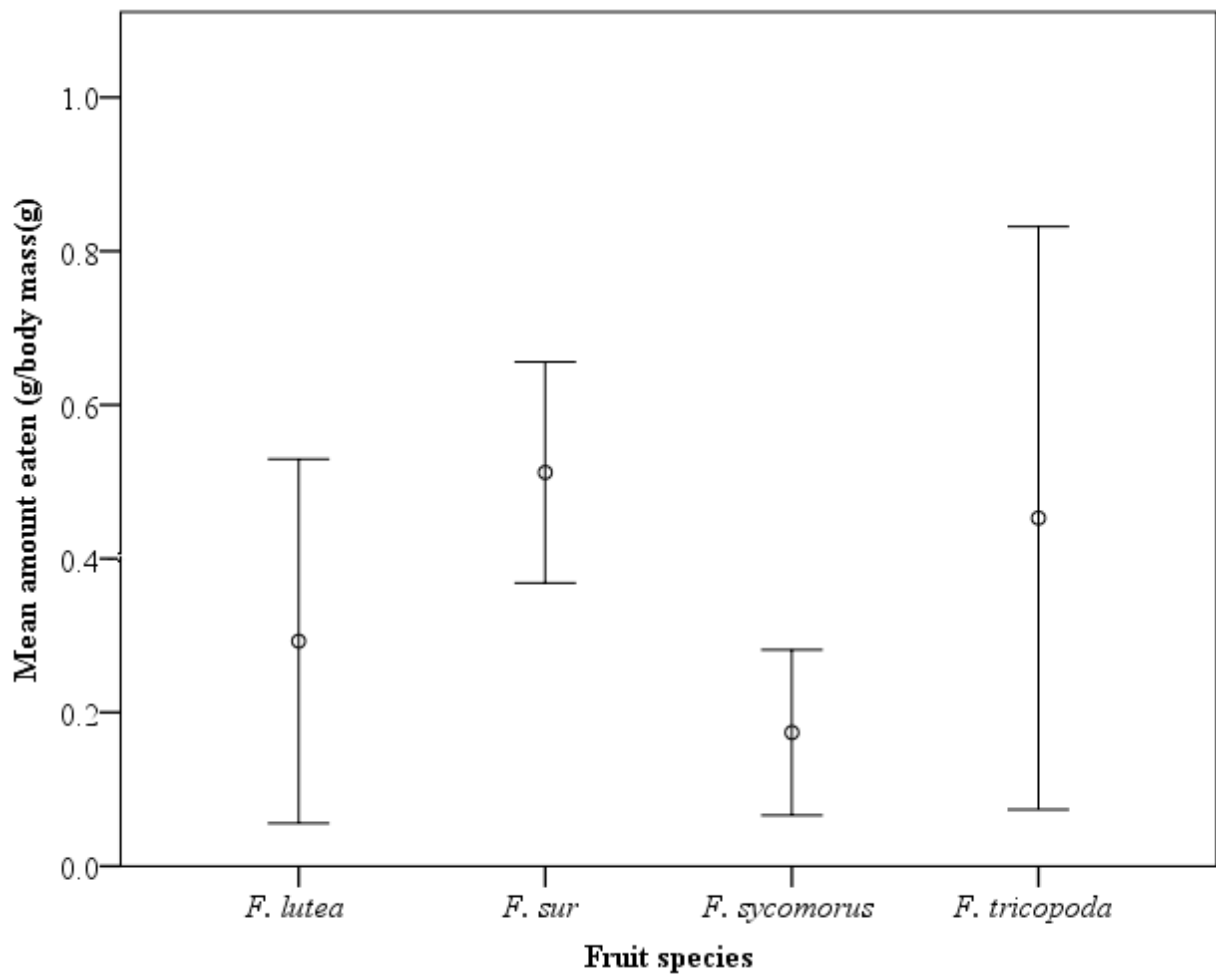
Fig. 4.1. Mean (± SE) mass of Ficus fruits per unit body mass consumed by Wahlberg's epauletted fruit bats for the respective species in the present study

4.4.2 Germination experiments

The mean cumulative germination proportion was calculated for fruit ingested by fruit bats, de-pulped and whole fruit seeds for each *Ficus* fruit species. Germination percentage success of ingested seeds was relatively higher than de-pulped, and whole fruit observed for the duration of the study, except for *F. lutea*, with high germination percentage for manually de-pulped (64%) than whole fruit (43%) and ingested seeds (35%) (Fig. 4.2). Seedling emergence of ingested seeds varied significantly between the *Ficus* fruits species (Kruskal–Wallis ANOVA, $H_3 = 22.06$, $p < 0.001$) (Fig. 4.3). Ingested seeds emerged earlier than whole fruit

and de-pulped for all *Ficus* species used in the study except for *F. lutea,* which emerged approximately the same time as whole fruit but earlier than de-pulped seeds. Ingested *F. lutea* seed started germinating after 12 days, while whole fruits started germinating after 13 days and de-pulped after 28 days

(b)

Cumulative proportion of seeds germinated

Days after planting

Treatments
— Depulped
······ Ingested
--- Whole
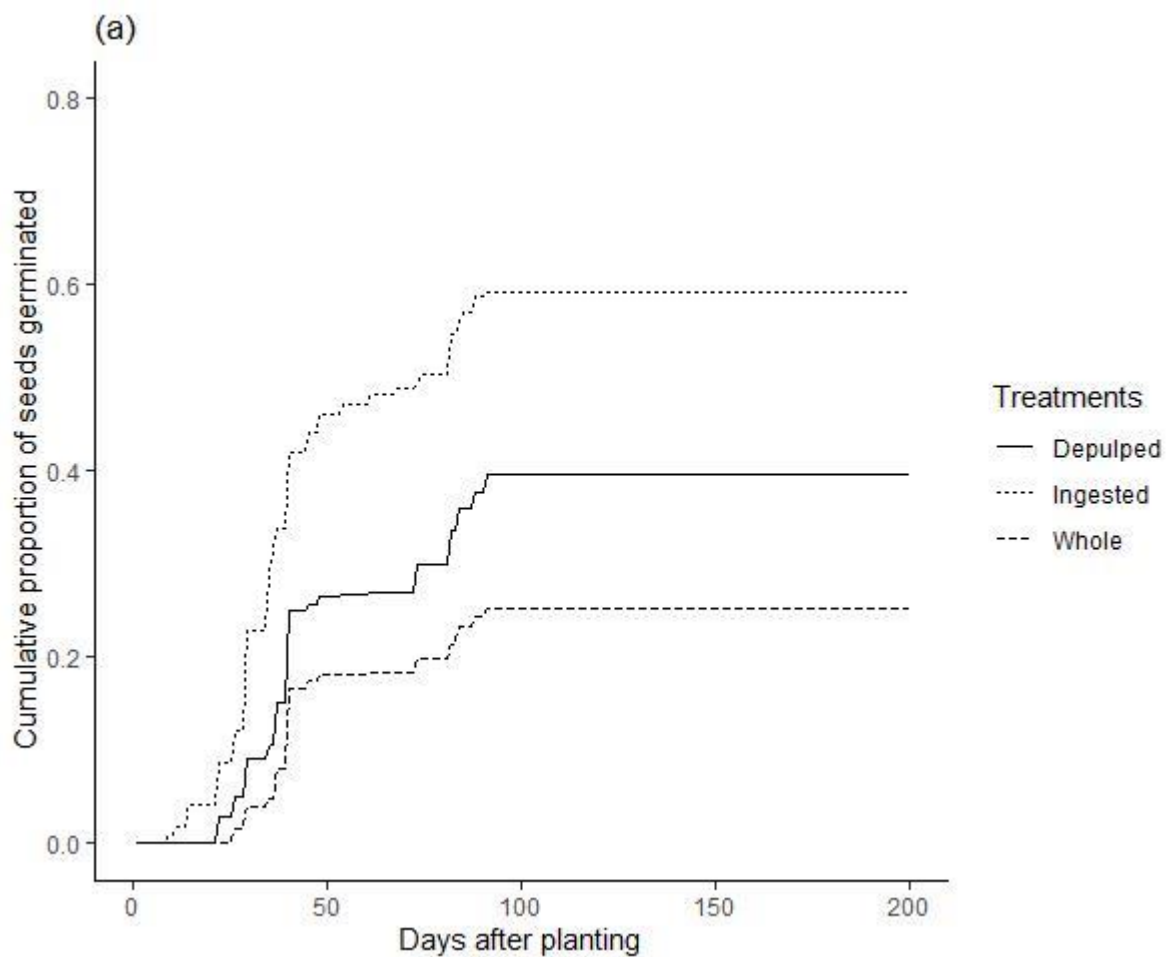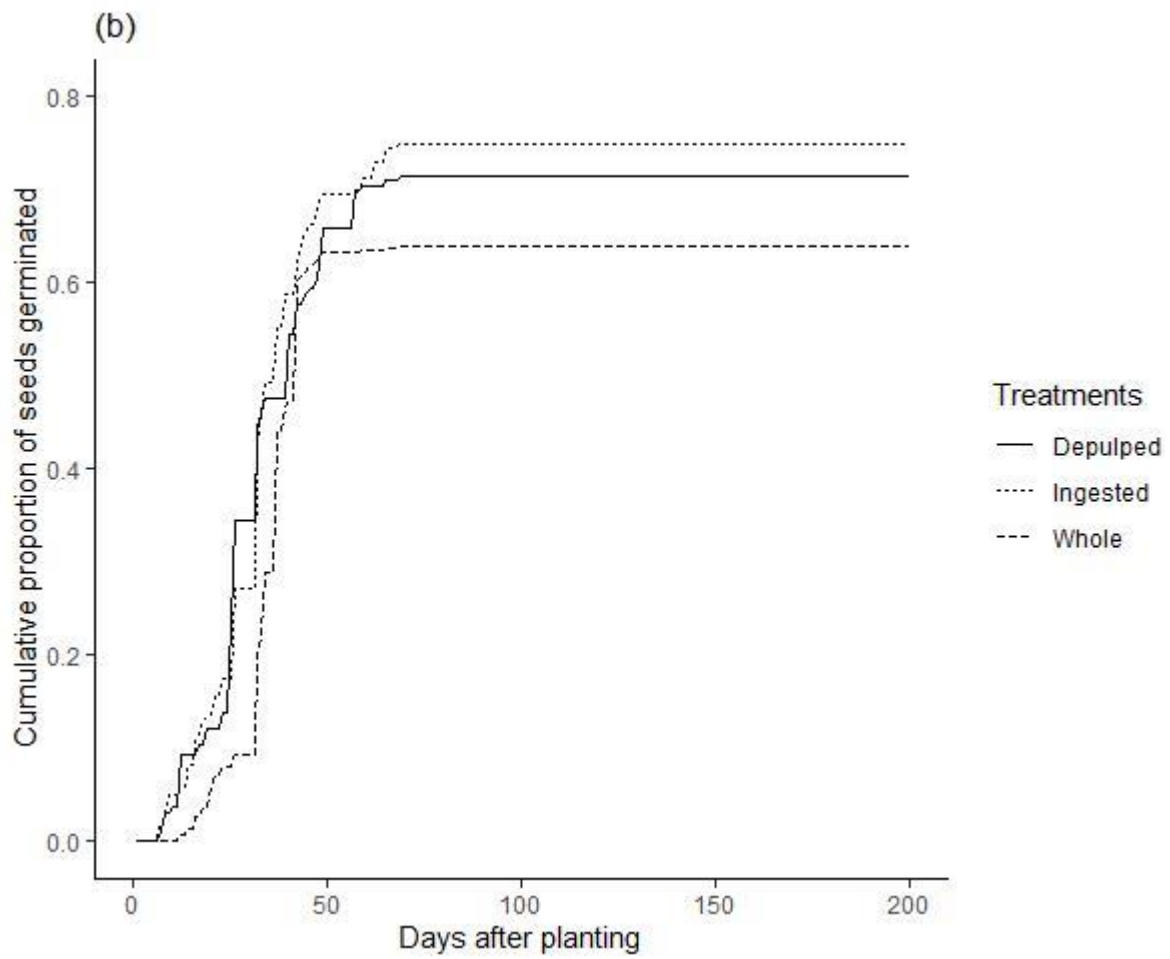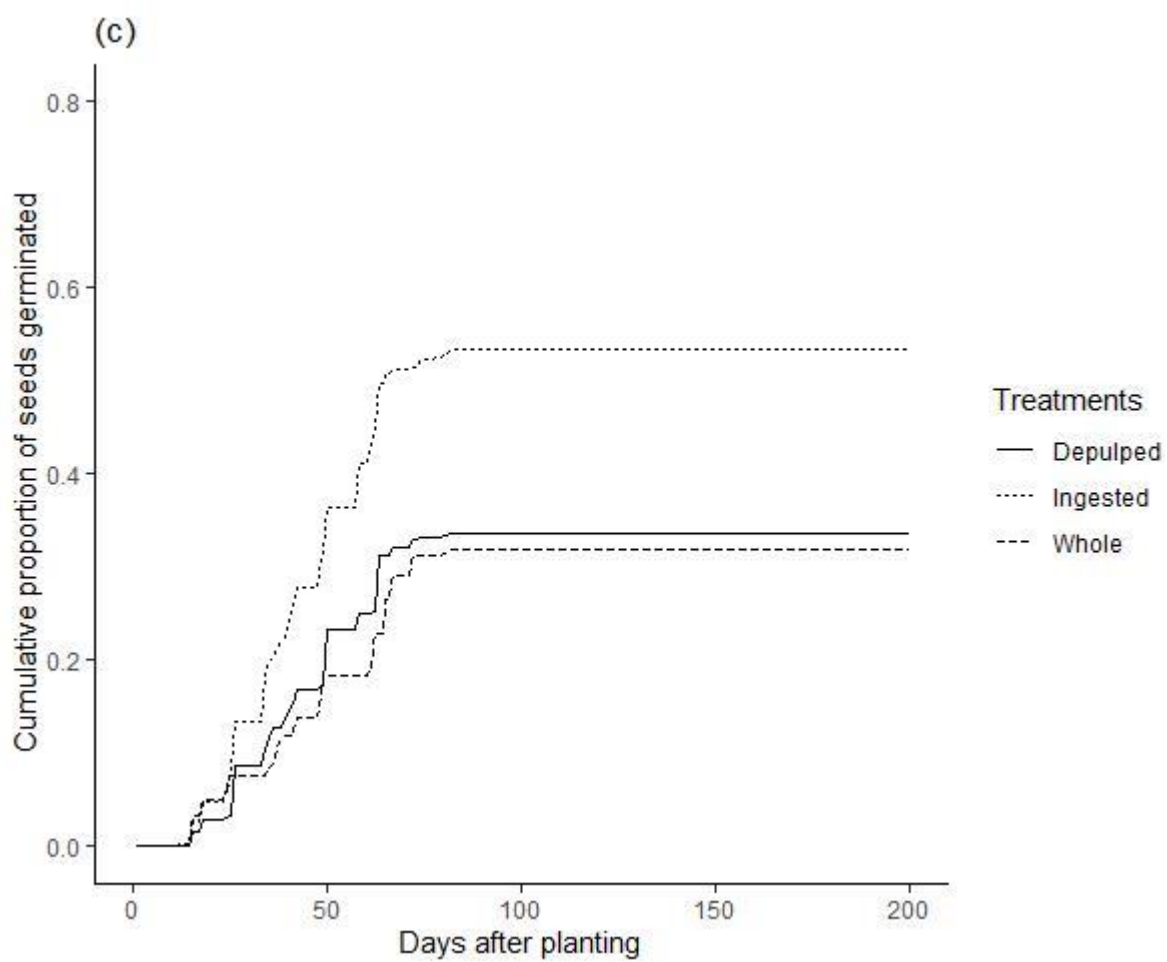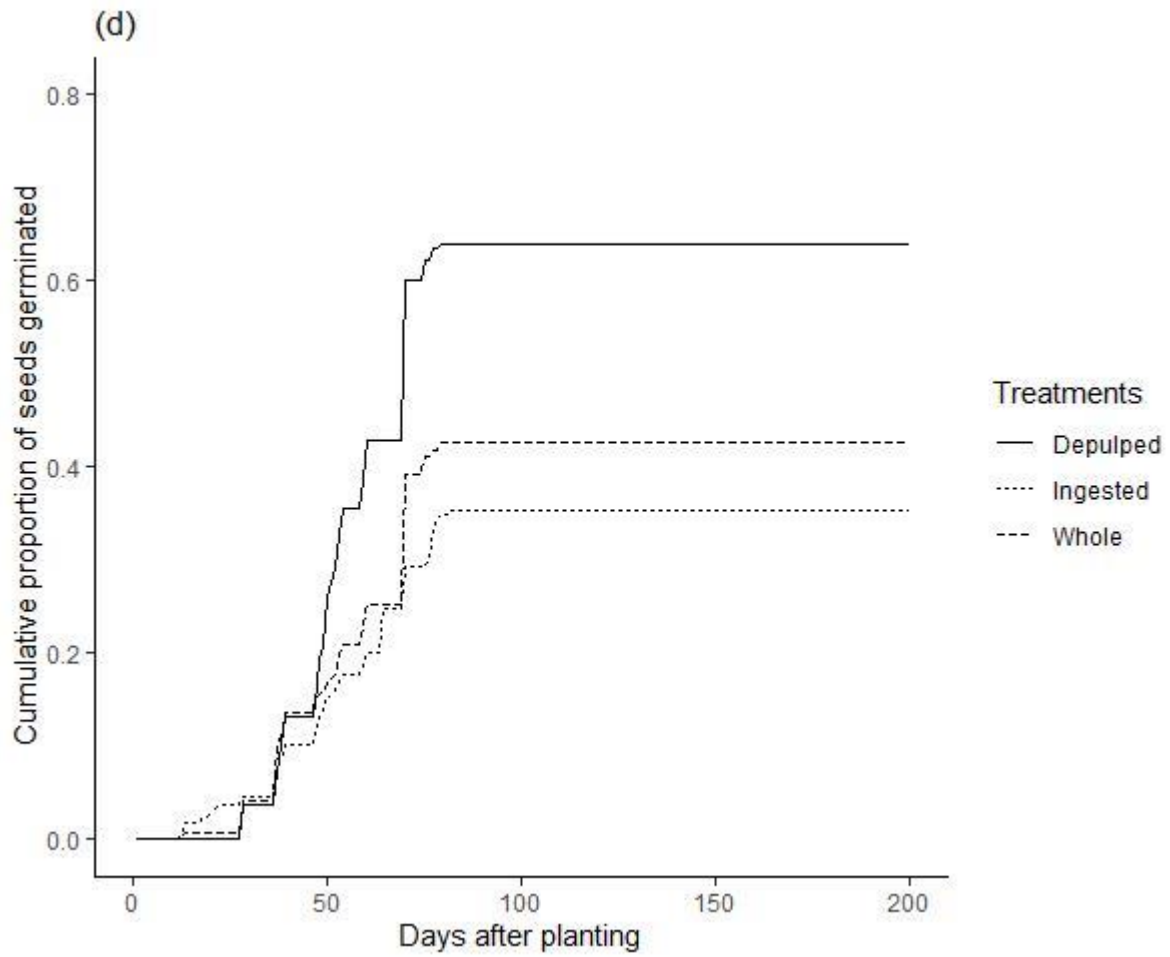
Fig. 4.2. Cumulative proportion germination of seeds ingested by Wahlberg's epauletted fruit bats, whole and de-pulped fruits for (a) *F. sycomorus*, (b) *F. sur,* (c) *F. tricopoda* and (d) *F. lutea* in the present study
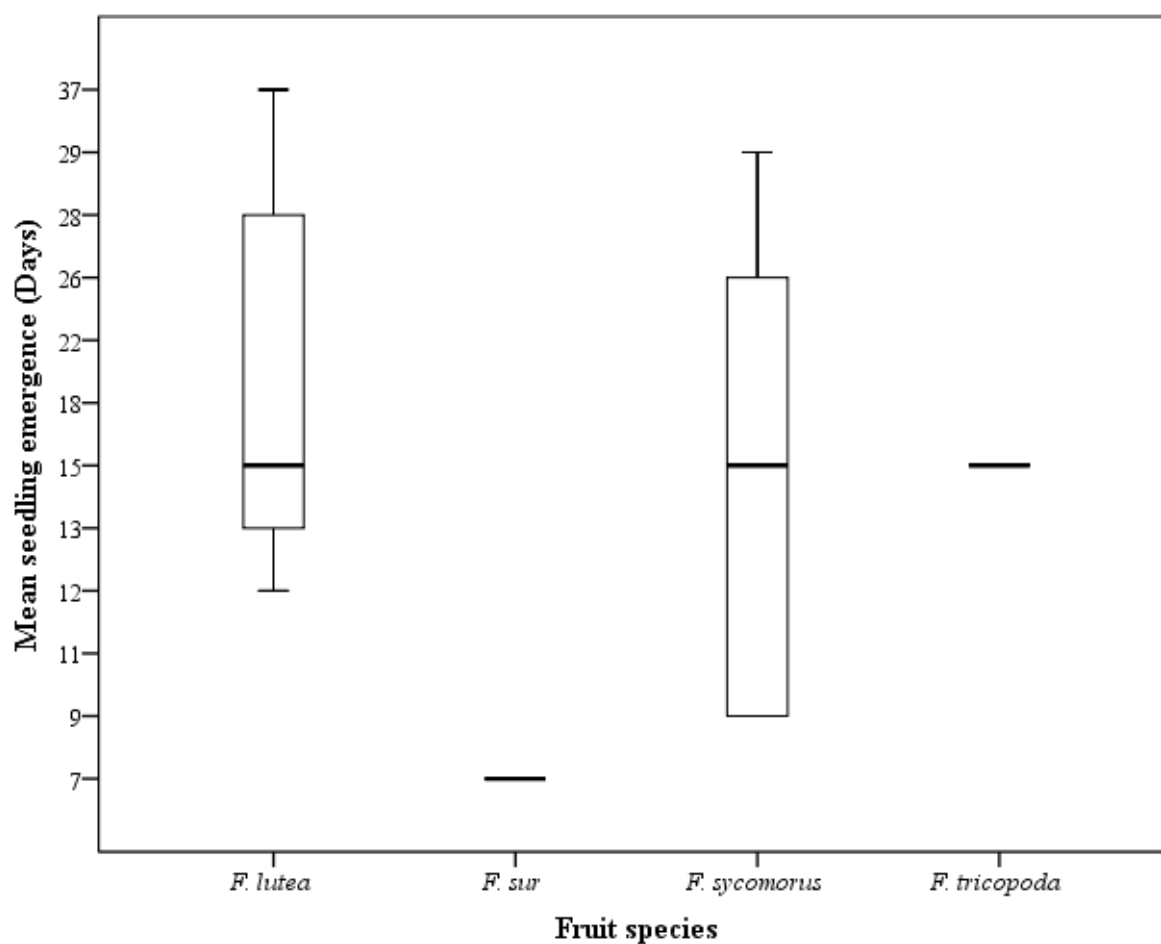
Fig. 4.3. Day of first seedling emergence for ingested seeds by Wahlberg's epauletted fruit bats, de-pulped and whole fruit treatments for the respective *Ficus* spp. fruit. (Boxes indicate the 25 and 75% quartiles; solid black squares the medians; and bars the 10 and 90% values)

4.5 Discussion

We found *E. wahlbergi* consumed significant amounts of the fruit of each of the *Ficus* spp. (Fig. 4.1, per gram body mass). This concurs with other studies that also reported that fruit bats species consume a significant amount of *Ficus* fruit daily especially relative to their body mass (Morrison 1980; Izhaki *et al*. 1995; Jordaan *et al*. 2012; Pulzatto *et al*. 2018). Our results showed that *E. wahlbergi* consumed up to 50% of their body mass when feeding on *Ficus* fruit. In comparison, Jordaan *et al*. (2012) reported that *E. wahlbergi* consumed more fruit mass than their body mass (per gram body, 110%). Izhaki *et al*. (1995) found that the Egyptian fruit bat *Rousettus aegyptiacus* consumed up to 150% of their body mass when feeding on *Eriobotrya japonica* fruits. Based on trends, morphological similarities and overlap of *R. aegyptiacus* and *E. wahlbergi* from previous fruit ingestion studies, *E. wahlbergi* play a similar and important role as dispersers of *Ficus* spp. fruits (Monadjem *et al*. 2010; Jordaan *et al*. 2012; Downs *et al*. 2021).

Relatively smaller seeds such as *Ficus* spp. seeds have been reported to remain in the gut of fruit bats for longer periods and are therefore transported further than larger seeds enhancing seed dispersal and may result in the production of seed rain (Tang *et al*. 2007). It has also been reported that fruit bats commute between fruiting trees and their feeding roosts and often defecate on their way to and from fruiting trees, thus depositing seeds along their way (Charles-Dominique 1986; Alcantara *et al*. 2000; Jordano & Schupp 2000; Muscarella & Fleming 2007; Tang *et al*. 2007; Seltzer *et al*. 2013; Rollinson *et al*. 2014; Pulzatto *et al*. 2018). The *E. wahlbergi* are reported to change roosts frequently (Fenton *et al*. 1985; Rollinson *et al*. 2014), enhancing seed transportation. In the case of *Ficus lutea* and other *Ficus* spp. used in our study, we suggest that fruit bats will disperse viable seeds through faeces and spats during flight as indicated in several studies (Izhaki *et al*. 1995; Shilton *et al*.1999; Tang *et al*. 2007;

Heer *et al*. 2010; Jordaan *et al*. 2012; Pulzatto *et al*. 2018). Tang *et al*. (2007) and Shilton *et al*. (1999) observed that captured fruit bats in cages defecated after the cages were cleaned, suggesting that fig seeds could be retained in the digestive tracts of fruit bats for longer periods and thus over long distances (Monadjem *et al*. 2010; Rollinson *et al*. 2013).

We found germination rates were significantly higher, and seedling emergence was earlier for *Ficus* fruit species ingested than whole and de-pulped fruit in our study, except for *F. lutea* (Fig. 4.2). These trends corroborate with past studies. For example, several studies (Lopez & Vaughan 2004; Tang *et al*. 2007; Pulzatto *et al*. 2018) showed that seeds of *Ficus* spp., such as *F. insipida*, *F. adhatodifolia, F. racemosa and F. luschnathiana,* ingested by fruit bats had positive and beneficial effects on germination rates than seeds not ingested. In addition, Heer *et al*. (2010) and Voigt *et al*. (2011) similarly reported that fruit bats positively influenced fig seed germination and dispersal by ingestion and pulp removal, while whole fruits failed to germinate because of fungal infection.

Beyond enhancing germination rates and the emergence of seedlings, studies have also suggested the importance of seed ingestion by fruit bat species for the restoration of degraded areas because they typically cover a relatively large area and long distances for foraging (Bernard & Fenton 2002; Heer *et al*. 2010; Trevelin *et al*. 2013; Pulzatto *et al*. 2018). This enhances gene flow between populations from different habitat fragments (Pulzatto *et al*. 2018). Our findings, as with previous studies, therefore, show the importance of fruit bats in seed dispersal, seed rain and restoration projects for degraded areas (Muscarella & Fleming 2007; Pulzatto *et al*. 2018). In particular, concerning keystone *Ficus* spp. which contribute substantially to ecosystem biomass, providing food for fruit bats, birds and other mammals (Shanahan *et al*. 2001; Kunz *et al*. 2011; Amponsah-Mensah *et al*. 2019). According to Jordaan *et al*. (2012), the role of *E. wahlbergi* as seed dispersers of fruits has been less studied and underestimated in South Africa than avian species, especially given the amounts they ingest

per day. Fruit bats use figs as sources of nectar and fruit and, in the process, function as pollinators and dispersers (Izhaki *et al*. 1995; Heer *et al*. 2010; Pulzatto *et al*. 2018). Our results and field observation (pers. obs.) during the study concur with other studies (Henry & Jouard 2007; Tang *et al*. 2007; Downs *et al*. 2010; Heer *et al*. 2010; Jordaan *et al*. 2012; Rollinson 2013; Trevelin *et al*. 2013; Pulzatto *et al*. 2018) emphasising the importance of fruit bats in improving germination, enhancing seed dispersal and restoration of degraded and urban areas as well as intact forests through seed rain.

4.6 Declarations

Conflict of Interest

The authors declare they have no conflicts of interest.

Ethics

All animal experiments were approved by the Animal research ethics committee, University of KwaZulu-Natal (reference no. 020/15/Animal). All applicable institutional and national guidelines for the care and use of animals were followed.

Author contributions

IAR and CTD conceived and designed the experiments. CTD sought funding, permits and ethical clearance. IAR performed the experiments. IAR analysed the data. IAR wrote the draft manuscript. CTD edited the manuscript.

Data availability

The data belong to the University of KwaZulu-Natal and are available from the corresponding author on reasonable request.

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CHAPTER 5

Fruiting phenology, diversity and distribution of native *Ficus* species in an urban-forest mosaic landscape in KwaZulu-Natal, South Africa

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Running header: Fruiting phenology, diversity and distribution of native *Ficus* species

5.1 Abstract

The genus *Ficus* is one of the largest genera of angiosperms, including species that grow as trees, shrubs, hemi-epiphytes, climbers, epiphyte, free-standing, and creepers. They are significant components of tropical and subtropical ecosystems, in terms of their copious aseasonal fruit production throughout the year. Ecologically, they are often keystone species, providing fruit for vertebrate frugivores, especially in times of food scarcity. Our research aimed to document the diversity, fruiting phenology and map the distribution of *Ficus* species in an urban-forest mosaic landscape in KwaZulu-Natal, South Africa. We recorded seven species and 478 individual fig trees in the urban-forest mosaic landscape of the study area. The most abundant fig tree species recorded across all land-use types was *F. natalensis* (124 stems, 26%), followed by *F. tricopoda* (110 stems, 23%) while *F. sur* (31 stems, 7%) was the least abundant. The urban built areas had the highest number (128) of fig trees, and most of the fig trees recorded in the forest nature reserves were along the forest edges, with relatively few figs inside the forests. Our results, therefore, presented valuable information for the management and conservation of these food resources and their dependant vertebrates in urban mosaic landscapes.

Keywords: Phenology, Distribution, figs, fruit, land-use, Urban mosaic landscape

5.2 Introduction

Ficus (Moraceae), commonly called figs, constitute one of the largest genera of angiosperms, with more than 850 species (Frodin, 2004; Ronsted et al., 2007; Chaudhary et al., 2012; Mabberley, 2017; Mohapatra et al., 2020). Figs display a wide range of life strategies, including species that grow as trees, shrubs, hemi-epiphytes, climbers, epiphytes and creepers occurring in the tropics and subtropics worldwide (Harrison & Rasplus, 2006; Wang et al., 2013). The African floristic region contains about 124 species of *Ficus* (Berg & Wiebes, 1992; Burrows & Burrows, 2003; Van Noort & Rasplus, 2020; Raji & Downs, in prep.).

Figs *(Ficus* spp.) are found in various habitats ranging from intact and human-modified landscapes (Berg, 1989; Burrows & Burrows, 2003; Tweheyo & Obua, 2003). They serve as an important part of biodiversity in the ecosystem by their all year round setting of fruit and provide food for a range of fruit-eating animals and seed dispersers (Shananhan et al., 2001; Ronsted et al., 2007; Walther et al., 2017). Various avian and mammalian species feed on the fruits, including birds (Shananhan et al., 2001; Walther et al., 2017), fruit bats (Izhaki et al., 1985; Tang, 2007; Heer et al., 2010), squirrels, civets (Lok et al., 2013) and primates (Gautier-Hion, 1980; Ruhiyat, 1983; Tweheyo & Obua, 2003; Hendrayana et al., 2019). Figs are also used as resting and nesting trees for fauna (Sinaga et al., 2012; Hendrayana et al., 2019).

Figs are distinguished from other plants by one unique taxonomic feature, common to all species: the syconium, characterised by its unusual, enclosed inflorescences after pollination, develops into compound accessory fruits (Compton & Greef, 2020). The syconium of a fig is a hollow, fleshy receptacle with only one hole at the tip called the ostiole or orifice enclosed by multiple inner brachtea with unisexual apetal flowers (Harrison & Rasplus, 2006; Wang et al., 2013; Wijaya & Defiani, 2021). The syconium releases a species-specific compound to attract

certain pollinators (Harrison & Rasplus, 2006; Wang et al., 2013; Wijaya & Defiani, 2021), after which the inner-brachtea stretches to form a small path for the pollinator (Harrison & Rasplus, 2006; Wijaya & Defiani, 2021).

The phenology of *Ficus* species is different from that of other tropical trees. Fig trees of the same species may be found with syconia in all phases of development, although a tree may have syconia in only one stage (Janzen, 1979; Tweheyo & Obua, 2003; Wijaya & Defiani, 2021). Fig fruits are small and are born on short peduncles in the leaf axis when young; their fruit crops can be as much as 500,000– to 1,000,000, with each fruit having a mean diameter of 10–50 mm (Janzen, 1979; Tweheyo & Obua, 2003; Foster, 2014). The different *Ficus* species produce fruits that vary in size and colour, favouring a range of vertebrate taxa (O'Brien et al., 1998; Shanahan et al., 2001; Kinnaird & O'Brien, 2005; Foster, 2014).

Fig trees have been reported to play an important role in ecological restoration (Slocum, 2001; Cottee-Jones et al., 2016). It has been found that the density and diversity of their saplings are two times higher than those from other genera, suggesting that they are more effective in restoring degraded ecosystems compared with other plants (Sreekar et al., 2010; Cottee-Jones et al., 2016; Hendrayana et al., 2019). Cottee-Jones et al. (2016) reported that the diversity index and dominance values of *Ficus* were higher than other taxa regarding the composition of vegetation communities. Consequently, *Ficus* species can support the regeneration of plant communities in a landscape that promotes the spread of fruiting plants and develops new composition structures (Corbin & Holl 2012; Cottee-Jones et al., 2016; Hendrayana et al., 2019). Such plant species that have important values in the composition and structure of a vegetation community are known to have key functionalities in tropical forest ecosystems and serve as a strong indicator of change in land uses (Hendrayana et al., 2019; Wijaya & Defiani, 2021).

Figs also have important roles in urban-forest areas. For example, they attract a range of taxa, including birds and mammals, and provide important food resources and habitats, so they are vital resources to maintain biodiversity (Chibesa & Downs, 2017; Lok et al., 2013; Lim et al., 2017; Walther et al., 2017). However, the survival of these taxa is attributed to be dependent on several other factors such as the availability of food supply, disparity in assemblages of predators, and risk of collision with anthropogenic structures (Shananhan et al., 2001). Therefore, it is of interest to understand the diversity and distribution of figs across different landscapes because it helps maintain ecosystem functioning and stability and is also important for environmental assessment (Shanahan et al., 2001; Harrison, 2005; Sreekar et al., 2010; Kuaraksa et al., 2012). We, therefore, predicted that the distribution of key food resources, figs, may be influenced by land-use changes across an urban-forest mosaic landscape. Given this, our study attempted to map the distribution of fig trees and document their diversity and fruiting phenology in the urban-forest mosaic landscape of Durban, eThekwini Municipality, KwaZulu-Natal, South Africa. We predicted more *Ficus* tree species in the forest areas, and that *Ficus* fruited occurred throughout the year.
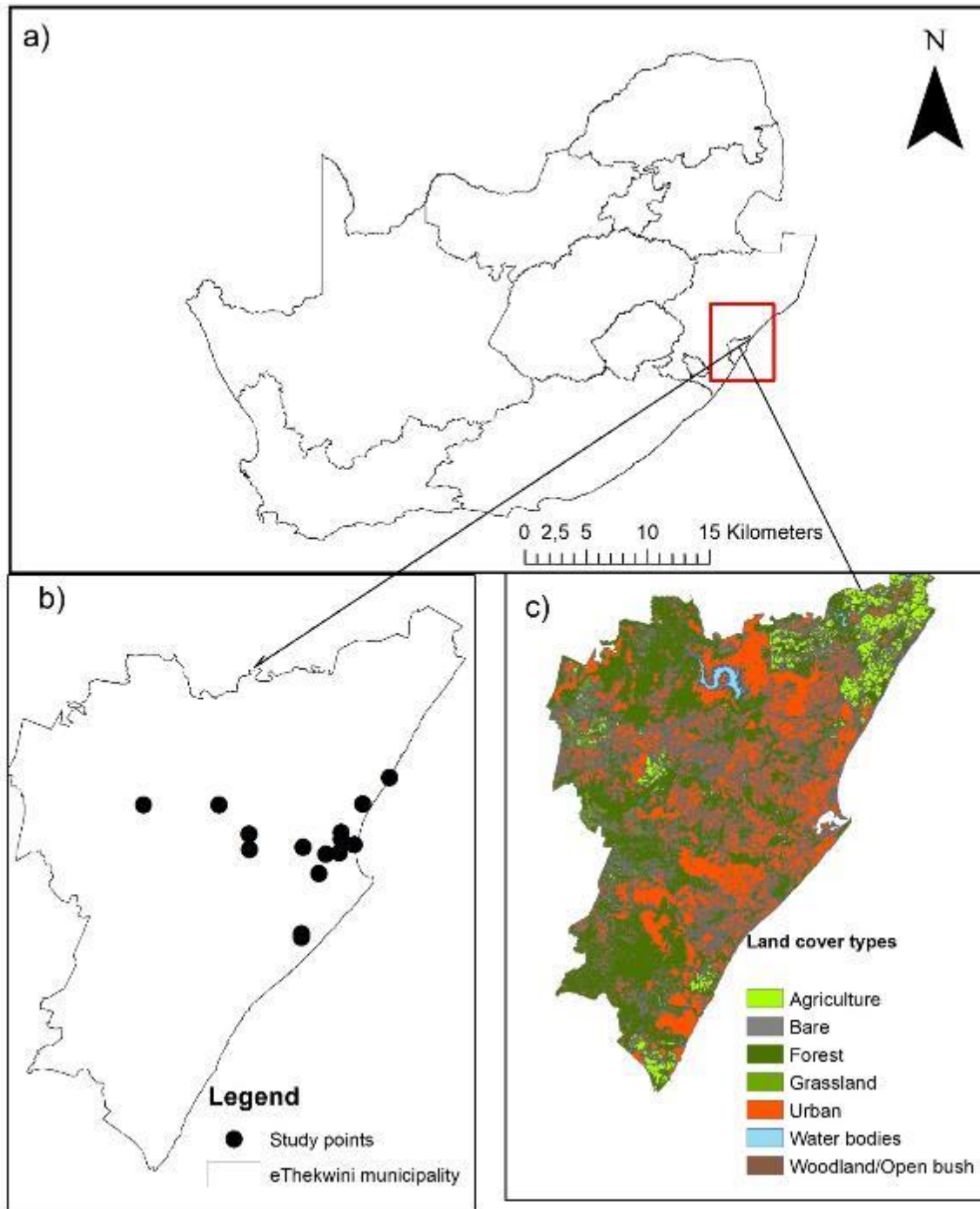
Fig. 5.1. Map showing the location of study area a) eThekwini Municipality KwaZulu-Natal Province, South Africa, b) Study area points in eThekwini Municipality, and c) the land-use cover types in eThekwini Municipality

5.3 Methods

5.3.1 Study area

KwaZulu-Natal Province is on the east coast of South Africa (29.8120° S, 30.8039° E, Fig. 5.1) and supports one-sixth of South Africa's remaining indigenous forest (Mucina & Rutherford, 2006: Ehlers Smith et al., 2017; Zungu et al., 2019). We conducted this study from August 2019 to January 2021 in the urban-forest mosaic landscape of Durban, eThekwini Municipality, KwaZulu-Natal. eThekwini Municipality is about 2297 km^2 in extent with the third-largest metropolitan area in South Africa and has the busiest port in Africa (EThekwini Municipality 2013; Zungu et al., 2019). The study area included part of the Durban Metropolitan Open Space System (D'MOSS), which consists of a landscape mosaic of built areas dominated by anthropogenic structures, open green spaces (managed and natural) and protected natural vegetation areas (McPherson et al., 2016; Maseko et al., 2019; Zungu et al., 2019; Shivambu et al., 2021; Supplementary Information Table S5.1).

5.3.2 Sampling procedures and data analyses

We placed articles in local newspapers, online platforms (Facebook) and conservancy websites to obtain information from local inhabitants (citizen scientists) on various *Ficus* species in urban areas of Durban, eThekwini Municipality. We got responses from conservancies and people living in built urban areas mainly. Although we got few responses from people in suburbia and townships, we obtained additional information on the distribution of *Ficus* species through face-face interviews during the sampling period. We, therefore, sampled a range of suburbia areas of Musgrave, Berea; Alipore area, Bluff; Sherwood; Merebank; Durban North; Mfishane; Cowey Road, Ruthleigh Drive, Uve Road, Umhlanga Rocks including nature reserves and sports park in

Durban, eThekwini Municipality (Fig. 5.1, Supplementary information Table S5.1). Based on the information gathered, we collected data on fig tree distribution, diversity, and fruiting phenology in the urban mosaic landscape of the municipality using systematic random sampling. A starting sampling point was selected at random. We then walked systematically through the streets, green spaces, landfill areas, nature reserves, and sports parks based on the information gathered from the citizen scientists and recorded the location of every fig tree found using a handheld global positioning system (GPSMAP 62sc Garmin International, Kansas, USA).

For each *Ficus* tree found, we recorded additional information, including whether it was fruiting or not and whether the fruit was ripe or not. We also recorded the height of the tree using an android application named "Measure" (version 2.5. 200124026, Google LLC, 2016) (Table 5.1). We identified figs using Burrows and Burrows (2003) and Boon and Pooley (2010) (Fig. 5.2). We digitised the geographical location data collected of each fig tree using ArcGIS (ver. 10.3.1, ESRI, Redlands, CA, USA) on the 2016 land cover map for KwaZulu-Natal, South Africa (GeoTerraImage, 2016). This enabled us to determine the spatial distribution of the figs sampled. We used an analysis of variance in R statistical software (version 3.6.1, R Core Team, 2018) to compare the fig tree abundance with land-use type in the urban-forest mosaic landscape.

To quantify the fruit crop size for fig trees, we divided the branches containing fruits into three main categories; primary, secondary and small branches. We then estimated the number of primary branches times the average number of secondary branches times the average number of small branches times the average number of fruits per branch following methods used previously (Korine et al., 2000; Tweheyo & Lye, 2003). For each species, these measurements were done for a minimum of ten individuals.

We defined the length of time with ripe fruit (ripening persistence) as the period (days) from the first observation of the appearance of ripe fruit to the time when less than 5% of the counted fruits remained on the focal tree branches (Korine et al., 2000). We visited each marked fig tree at least twice a month to monitor its fruiting phenology and ripening persistence (Table 5.1). We used descriptive statistics to analyse these data. Data are presented as Means ($\pm$ SD).

5.4 Results

We recorded seven species and 478 individual fig trees in the urban-forest mosaic landscape of our study area in eThekwini Municipality. These included (a) *Ficus natalensis,* (b) *F. lutea,* (c) *F. sycomorus,* (d) *F. tricopoda,* (e) *F. polita,* (f) *F. sur* and (g) *F. burkei*. The most abundant fig tree species recorded across all land-use types was *F. natalensis* (124 stems, 26%) followed by *F. tricopoda* (110 stems, 23%) while *F. sur* (31 stems, 7%) was the least abundant (Supplementary information Fig.S5.1 and Tables S5.1-S5.2). The urban built areas had the highest number (128) of fig trees (Fig. 5.3; Supplementary Tables S5.1-S5.2). In addition, the highest number of fig species were recorded in the urban built areas (n = 7 species) and nature reserves (n = 7 species). Information gathered from citizen scientists revealed that some of the fig trees in the urban built area were planted. We recorded most of the fig trees in the nature reserves along the forest edges, with relatively few figs inside the forests. We found no significant difference in the number of fig trees with land-use type in the urban-forest mosaic landscape of the study area (ANOVA, $F_{4,30} =$ 0.52, $P > 0.05$, Supplementary information Table S5.2).

The ripening persistence of *Ficus* fruits ranged from 14-20 days (Table 5.1). According to our observations and data collected (Table 5.1), fruit-ripening persistence depended on fruit sizes. Fruits of *F. natalensis*, *F. burkei,* and *F. tricopoda* with relatively smaller fruit sizes took an

average of two weeks to ripen ($\pm$ 14 days, Table 5.1), while other species with larger fruit size had a longer ripening time. Fig fruits were available throughout the 18 months sampling period (Supplementary information Table S5.3). However, *F. lutea* and *F. tricopoda* were not fruiting between February-April of the sample period. Whereas *F. natalensis*, *F. sur,* and *F. sycomorus* had fruits throughout the year (Supplementary information Table S5.3) though not all individual trees fruited simultaneously. The total number of fig fruits available (crop size) recorded varied between 1780 and 48550 per monitored tree (Supplementary information Table S5.4)
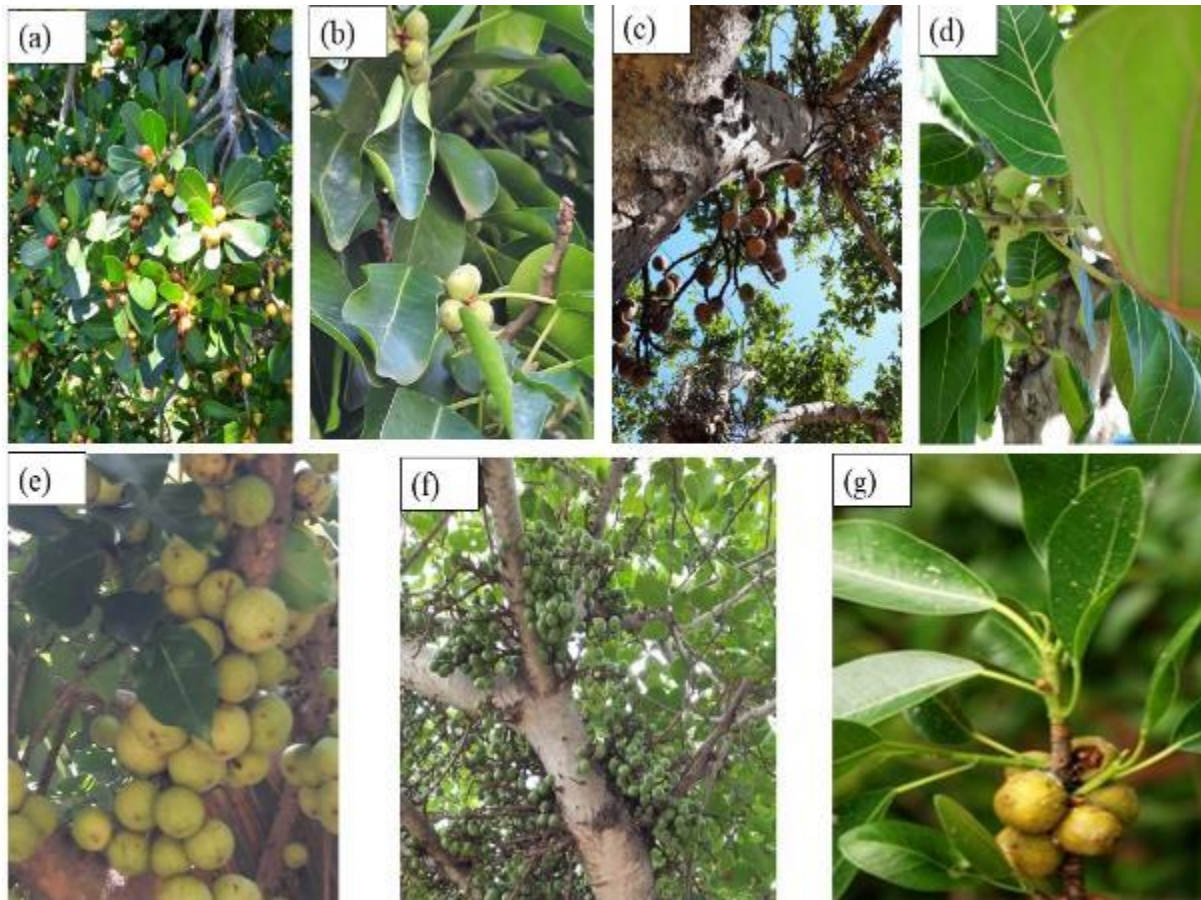
Fig. 5.2. Fig species in the study area (a) *Ficus natalensis*, (b) *Ficus lutea*, (c) *Ficus sycomorus*, (d) *Ficus tricopoda*, (e) *Ficus polita*, (f) *Ficus sur*, and (g) *Ficus burkei*

Table 5.1 Characteristics of fig trees species documented in the present study.

Genus-Ficus	Species	Common name	Fruiting period	Fruit size (mm diameter)	Fruit colour when ripe	Mean ($\pm$ SD) crop size	Mean ($\pm$ SD) persistence of ripening days	Height (m)
Subgenus								
Sycomorus	*Ficus sur*	Broom Cluster Fig	All year	20-40	Orange-red	24,640 $\pm$ 12800	18 $\pm$ 3	15-25
Urostigma	*Ficus natalensis*	Natal Fig	All year	10-20	Reddish-brown	40,000 $\pm$ 7565	14 $\pm$ 3	15-30
Urostigma	*Ficus lutea*	Giant-leaved Fig	May-January	15-30	Yellowish-brown	22,465 $\pm$ 9419	18 $\pm$ 3	15-25
Sycomorus	*Ficus sycomorus*	Common Cluster Fig	All year	20-50	Yellowish-red	20,000 $\pm$ 11082	18 $\pm$ 2	15-35

Urostigma	*Ficus burkei*	Strangler fig, common wild fig	January-October	10-20	Reddish-brown	42,460 $\pm$ 7035	14 $\pm$ 3	15-25
Urostigma	*Ficus polita*	Heart-leaved fig	August-February	20-40	Purple-green	20,000 $\pm$ 8891	20 $\pm$ 4	15-30
Urostigma	*Ficus tricopoda*	Swamp fig	May-January	15-35	Greenish-red	22,720 $\pm$ 5810	14 $\pm$ 3	15-25
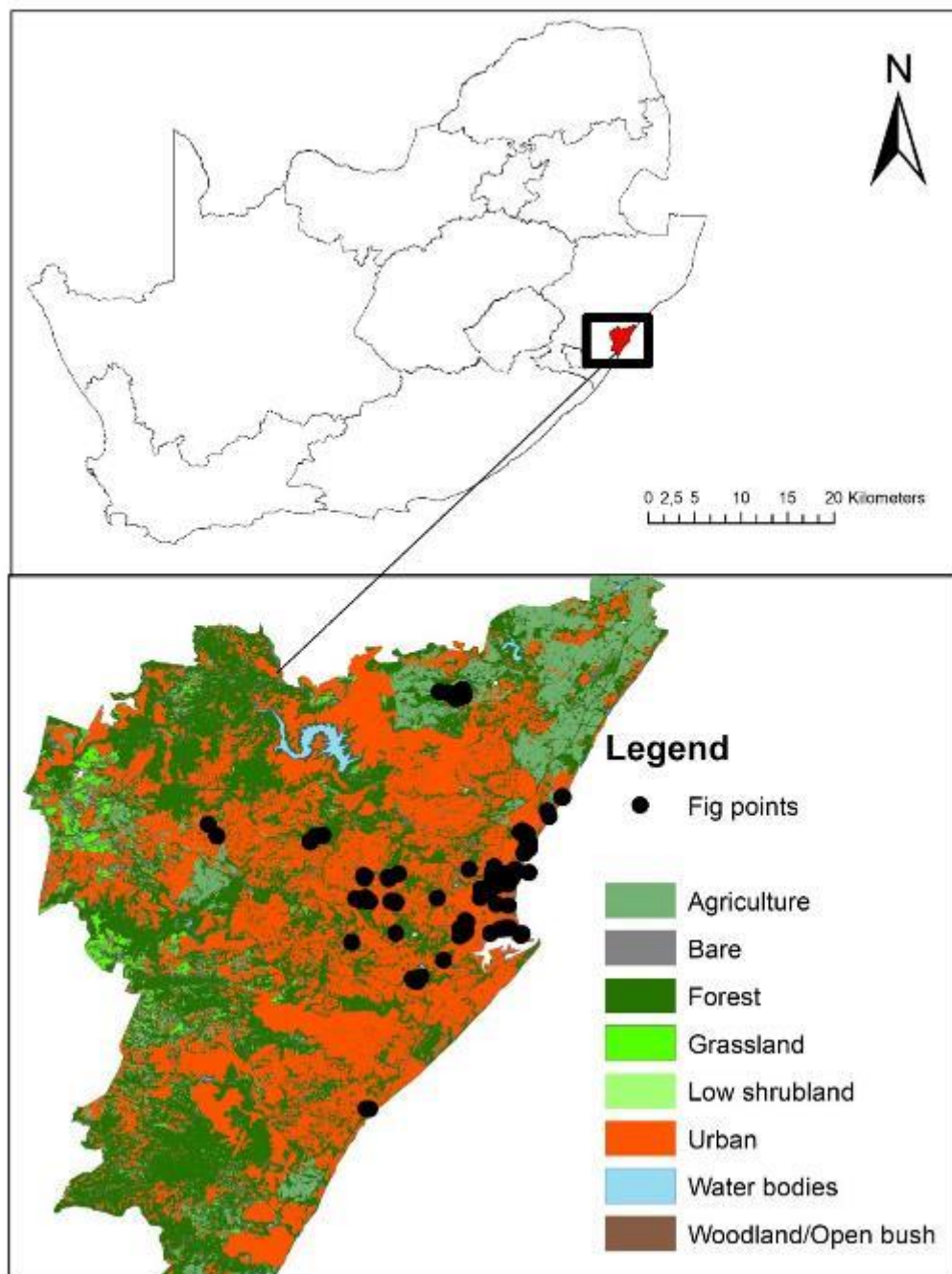
Fig. 5.3. The distribution of *Ficus* tree species with land-use types in the urban-forest mosaic landscape of eThekwini Municipality, Durban, KwaZulu-Natal, South Africa in the present study. (Note: Urban refers to urban built areas).
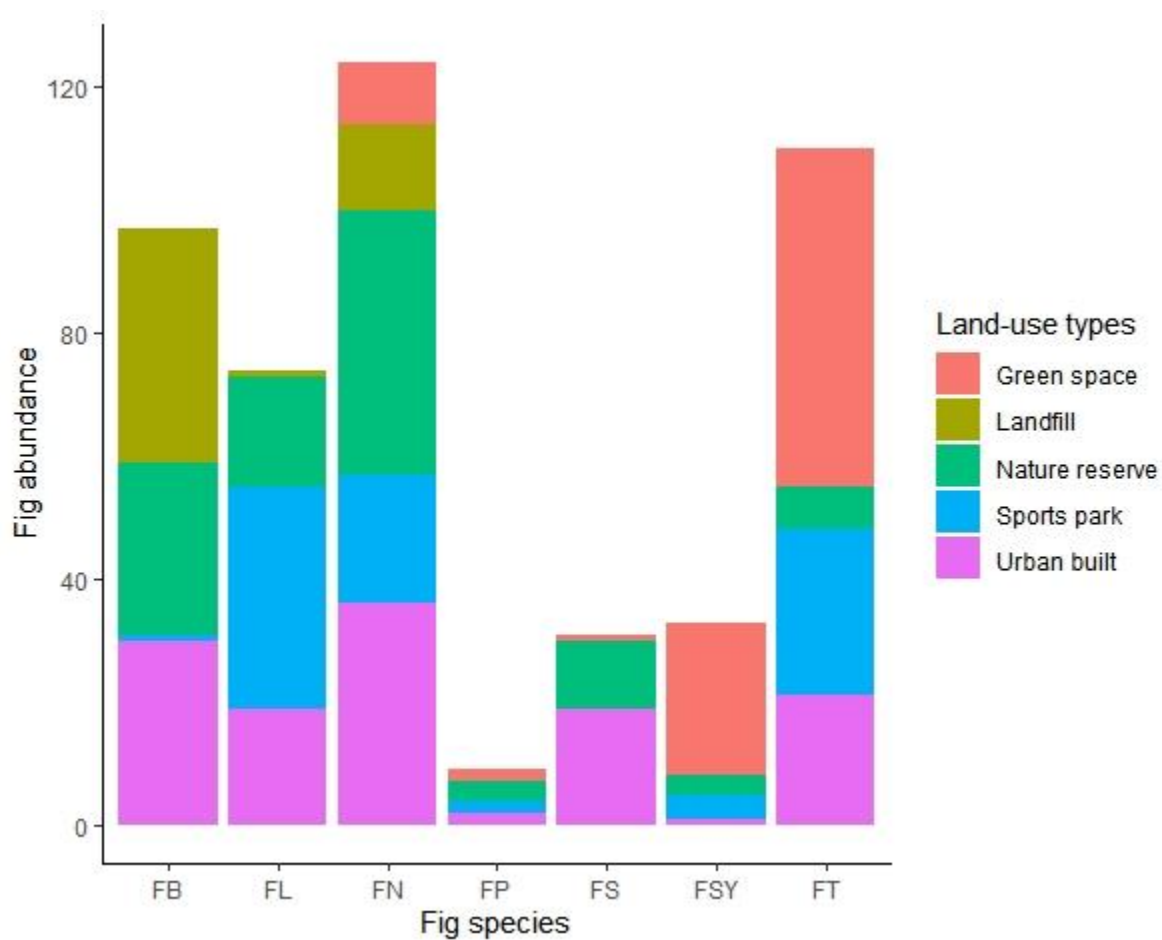
Fig. 5.4. The *Ficus* tree species (FB; *Ficus burkei*, FL; *Ficus lutea,* FN; *Ficus natalensis,* FP*; Ficus polita,* FS; *Ficus sur,* FSY; *Ficus sycomorus,* FT; *Ficus* tricopoda) abundance with land-use type in the urban-forest mosaic landscape of eThekwini Municipality, Durban, KwaZulu-Natal in the present study.

5.5 Discussion

Our observations of fig trees aseasonal fruiting ability (Table 5.1, Supplementary information Table S5.3) in a forest-urban landscape mosaic supported their attributed keystone species roles

and corroborated with other studies (Korine et al., 2000; Bleher et al., 2003). Furthermore, the asynchronous ripening pattern in fruited figs in our study showed a "steady state" availability of fruits for some species of figs over a long period (14-20 days, Table 5.1) and all year round. These fruiting cycles made them important food resources for several frugivores (pers. obs., unpublished data), as shown in other studies (Lambert & Marshall, 1991; Korine et al., 2000; Tang et al., 2007; Ranganathan & Borges, 2009; Ranganathan et al., 2010; Borges et al., 2011). For example, individuals of *F. natalensis*, *F. sur,* and *F. syncomorus* fruited each month of our study period. In addition to the fruiting availability of figs, studies have shown that fig fruit contains a range of essential nutrients and minerals (O'Brien et al., 1998; Korine et al., 2000; Shanahan et al., 2001; Acipa et al., 2013; Compton & Greef, 2020). The fruits of fig species recorded in our study were of different colours, fruit sizes with large and rewarding fruit crops (Table 5.1). This showed that they are vital in supporting diverse groups of frugivores (e.g., fruit bats, birds and primates, pers. obs.) as shown in other studies (Kalko et al., 1996; Cottee-Jones et al., 2016). Furthermore, colourful figs are likely to stand out because they are presumably easier to be detected by frugivores. Typically, fig fruits sizes are positively correlated with different sized frugivores (Kalko et al., 1996; Korine et al., 2000)

In other urban environments, native figs are important resources to maintain biodiversity (Lok et al., 2013; Lim et al., 2017; Walther et al., 2017). The figs in urban built and forest areas in the urban mosaic landscape are important sources of food, nesting sites and shelter to various vertebrate and invertebrate fauna (Corlett 2005, 2006; Acar et al., 2007; Stagoll et al., 2012; Lok et al., 2013; Somme et al., 2016). Information from citizen scientists confirmed that some fig trees in the urban mosaic landscape of eThekwini Municipality, such as managed green spaces (Umgeni Bird Park) and sports parks, were planted. They thereby provide food resources for biodiversity

and provide aesthetic features and shade in the environments where they grew. Similarly, Fernandez-Juricic and Jokimäki (2001) reported that vegetation in urban parks consisting of fig trees was often planted for aesthetic and restoration reasons. This typically acted as refugia and food resources for native species in urban mosaic landscapes, especially urban built areas (Fernandez-Juricic & Jokimäki, 2001).

Although we found no significant difference in the distribution of fig trees with land-use, our study found many fig trees in the urban built areas. Fig trees recorded in the forest nature reserves were scattered and typically found at the forest edges. According to Cottee-Jones et al. (2016), they can serve as a low-cost strategy to accelerate forest recovery and act as seedling recruitment foci. Also, by attracting seed dispersers, they enhance the dispersal of non-fig species to these areas. Due to the prolific fruiting of fig trees as found in our study, they have an excellent ability to support the regeneration of plant communities that are representative of the general landscape and influencing plant community composition and rates of succession as found in other studies (Galindo-Gonzalez et al., 2000; Holl et al., 2000; Schlawin & Zahawi, 2008; Corbin & Holl, 2012; Cottee-Jones et al., 2016). The results presented in this study are of value in the management and conservation of these food resources and their dependant vertebrates in urban mosaic landscapes.

5.6 Declarations

Acknowledgements

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Conflicts of Interest

The authors declare no conflict of interest.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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5.8 Supplementary information

n = **478**

Legend:
- Ficus burkei
- Ficus lutea
- Ficus natalensis
- Ficus polita
- Ficus sur
- Ficus sycomorus
- Ficus tricopoda
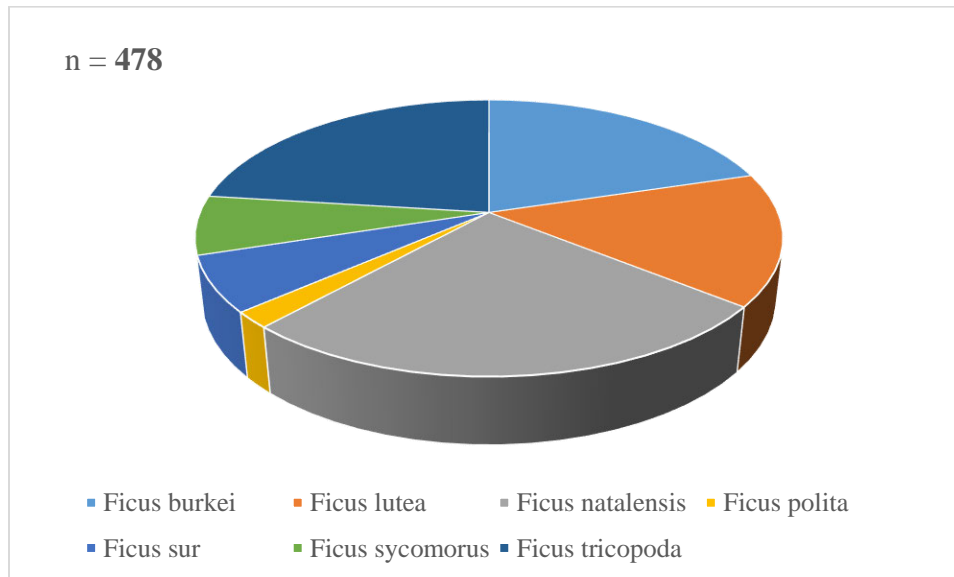
Supplementary Information Fig. S5.1. Proportion of *Ficus* species in the urban-forest landscape mosaic of eThekwini Municipality, Durban, KwaZulu-Natal, South Africa, in the present study.

Supplementary information Table S5.1. Land-use types and locations of fig trees distribution in the study

Land-use types	Locations
Landfill	Inanda farm (Buffelsdraai)
Managed green space	Umgeni Bird Estuary and area
Nature reserve	New Germany, Virginia Bush Reserve, Paradise Valley Reserve, Pigeon Valley Reserve, Burman Bush Reserve, Amanzimtoti Bird Sanctuary
Sports park	Golf Course Beach, South Beach
Urban built	Commercial areas and residential properties (which included surburbia such as the Musgrave area, Berea; Alipore area, Bluff; Sherwood; Merebank; Ruthleigh Drive, Durban North, Mfishane, Uve Road, Cowey Road, and Umhlanga Rocks)

Supplementary information Table S5.2. Number of native fig trees recorded across different land-uses in eThekwini Municipality. (See Supplementary information Table S5.1 for land-use types).

Ficus species	Land-use types				
	Landfill	Managed green space	Nature reserve	Sports park	Urban built
F. burkei (FB)	38	0	28	1	30
F. lutea (FL)	1	0	18	36	19
F. natalensis (FN)	14	10	43	21	36
F. polita (FP)	0	2	3	2	2
F. sur (FS)	0	1	11	0	19
F. sycomorus (FSY)	0	25	3	4	1
F. tricopoda (FT)	0	55	7	27	21

Supplementary information Table S5.3. Fruiting phenology and characteristics of *Ficus* species in the present study.

Scientific name	Common name	Ripe fruit colour	Fruiting period											
			Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Ficus lutea	Giant-leaved Fig	Yellowish-brown	X				X	X	X	X	X	X	X	X
Ficus natalensis	Natal Fig	Reddish-brown	X	X	X	X	X	X	X	X	X	X	X	X
Ficus sur	Broom Cluster Fig	Orange-red	X	X	X	X	X	X	X	X	X	X	X	X
Ficus sycomorus	Common Cluster Fig	Yellowish-red	X	X	X	X	X	X	X	X	X	X	X	X

Species	Common name	Colour												
Ficus trichopoda	Swamp fig	Greenish-red	X				X	X	X	X	X	X	X	X
Ficus polita	Heart-leaved fig	Purple-green	X	X						X	X	X	X	X
Ficus burkei	Strangler fig, common wild fig	Reddish-brown	X	X	X	X	X	X	X	X	X	X		

Supplementary Information Table S5.4. Selected trees recorded for fruiting phenology assessment

Fig species	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10
Ficus sur	23550	27760	5680	26840	7080	30980	20580	24530	27850	51550
Ficus natalensis	47570	38570	48550	35950	38650	35980	43980	29850	29750	51150
Ficus lutea	23450	27740	5880	26640	9280	20150	20280	24830	27850	38550
Ficus sycomorus	20805	32640	20130	7600	6505	22250	1780	27760	30980	29550
Ficus burkei	43570	39350	48550	47850	50850	38800	46980	32950	29750	45950

Ficus polita	24805	30120	29010	19650	0	14250	14680	20560	20380	26550
Ficus tricopoda	20850	29550	14880	26940	19280	22260	13280	22730	27880	29550

CHAPTER 6

Tree visitation and potential seed dispersal of keystone *Ficus* species by vertebrates in an urban mosaic landscape in eastern South Africa

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Running header: Urban vertebrate *Ficus* tree visitation and feeding

6.1 Abstract

Globally with the human population increase, urban expansion has increased, impacting biodiversity and ecosystem functions. Visitation of fruiting trees by vertebrate frugivores can influence the persistence of fleshy fruited trees and so further maintain frugivore communities in transformed landscapes. Figs (*Ficus* spp.) have been recognised as keystone plant resources that support diverse vertebrate frugivores communities. Our objective in this study was to examine the use of keystone *Ficus* species by vertebrate frugivores and their potential role as seed dispersers in the urban mosaic landscape of Durban, Ethekwini Municipality, KwaZulu-Natal, South Africa. We placed camera traps focused on focal fig trees to investigate how frugivore vertebrates use them. We quantified the diurnal and nocturnal frugivore visitation rates and interactions (birds, monkeys and bats). We analysed frugivore visits to 12 individual trees of five *Ficus* species, observed between 2019-2020. During 3888h, we recorded a total of 4,071 videos from camera traps with 10,016 visits and interactions between three main vertebrate taxa (8958 fruit bat visits, 808 bird visits and 250 monkey visits). These were in five *Ficus* species (*F. burkei, F. lutea, F. natalensis, F. sur* and *F. sycomorus*). We identified a total of 32 bird species visiting. We recorded a total of 8958 visits by Wahlberg's epauletted fruit bats *Epomophorus wahlbergi,* and 250 visits by vervet monkey *Chlorocebus pygerythrus*. The latter tended to stay for prolonged periods in the trees feeding. Our data showed the importance of fruiting fig trees for vertebrate frugivores in the urban mosaic landscape. This highlights the conservation implications for figs as keystone resources in the urban mosaic landscape. Our findings support the planting and conservation of *Ficus* tree species in transformed urban mosaic landscapes for the persistence of forest species biodiversity.

Keywords: Camera traps, frugivore, visitation, foraging behaviour, seed dispersal, figs, urban-forest gradient

6.2 Introduction

The human population has undergone a dramatic increase with a concomitant increase in urban expansion over the years (Grimm et al., 2008; Montgomery, 2008; McDonnell and Hahs, 2013; United Nations, 2018; Collins et al., 2021), although pressure resulting from this urbanisation is not uniformly distributed (Downs et al., 2021). The relatively fast disappearance of forests and rapid extinction of associated biodiversity is correlated with the human population increase, thus exerting continued pressures on natural resources (Pimm et al., 2014; Zungu et al., 2019). Land-use changes can profoundly affect biodiversity, particularly plant-frugivore interactions (Santos and Telleria, 1994; Farwig et al., 2006; Kirika et al., 2008; Grünewald et al., 2010).

Urban green spaces and nature reserves act as a refuge for fleshy fruited plant species in densely populated areas (Cottee-Jones et al., 2015; Eshiamwata et al., 2006; Lok et al., 2013; Matthews et al., 2017). The composition and structure of vegetation in these areas determine frugivores' presence and absence (Forman, 2016; Gallo et al., 2017; Grimm et al., 2000; Lopucki and Kitowski, 2017; Collins et al., 2021). Consequently, areas that retain fleshy fruited plants generally have more frugivorous species persisting (Chace and Walsh, 2006; Cottee-Jones et al., 2015; Eshiamwata et al., 2006; Lok et al., 2013; Matthews et al., 2017). Globally, it has been estimated that vertebrates frugivores disperse about 90% of trees and shrubs in tropical regions (Shanahan et al., 2001; Mokotjomela et al., 2013). Many fleshy fruited plants rely on these vertebrates to dispersal their seeds (Jordano, 2000; Shanahan et al., 2001; Mokotjomela et al., 2013). However, the survival of frugivores in urban-mosaic landscapes is controlled by several factors such as the availability and supply of food, variation in predator assemblages, and risk of collision with anthropogenic structures (Chace and Walsh, 2006; Chibesa and Downs, 2017).

Figs (*Ficus* spp; Moraceae) have been regarded as a critical plant resource throughout the tropics, with fruits available all year-round and been eating by many vertebrates (Shanahan et al., 2001; Bleher et al., 2003; Walther et al., 2018; Chong et al., 2021). Fleshy fruited figs are suitable for animal consumption, maintaining their dispersal population (Howe and Smallwood, 1982; Kissling, 2009; Lomáscolo et al., 2010; Aziz et al., 2021). Fig trees attract a range of animals, with over 10% of the world's birds and 6% of mammals consuming fig fruit. Therefore, several researchers recommend *Ficus* tree species for reforestation and restoration programmes (Shanahan et al., 2001; Cottee-Jones et al., 2016; Kuaraksa et al., 2012; Zahawi and Leighton Reid, 2018; Chong et al., 2021).

The keystone function of figs to vertebrates in tropical urban mosaic landscapes is yet to be adequately researched (Cottee-Jones et al., 2016; Chong et al., 2021). Thus, with the use of camera traps, we investigated frugivore visits to fig trees and their potential role as seed dispersers in an urban mosaic landscape, including nature reserves, managed green spaces and urban built areas. Our main objective was to identify the frugivores vertebrates visiting fruiting *Ficus* trees as a potential guide for future conservation and management programmes. We assessed the importance of the fruiting *Ficus* tree species by recording all the interactions (visits) that occurred when frugivores visited (i.e. flight, perch, peck, and eat). We also noted the behaviour of the visitor on the tree and if fruits were consumed. We predicted a range of vertebrate species would visit the fruiting *Ficus* tree species in the urban mosaic landscape. We also predicted that fruit bats would likely be the most common vertebrate taxon visiting the fruiting *Ficus* trees in the urban mosaic landscape despite other vertebrate frugivore taxa persisting in this landscape (Downs et al. 2021).

6.3 Methods

6.3.1 Study area and species

We conducted our study between August 2019 and November 2020 in the urban mosaic landscape of Durban, Ethekwini Municipality, KwaZulu-Natal, South Africa (29.8120° S, 30.8039° E, Fig. 6.1). This includes natural forest urban gradients. The area includes nature reserves, managed green spaces (gardens and parks) and urban built areas dominated by anthropogenic structures (McPherson et al., 2016; Maseko et al., 2019; Zungu et al., 2019).

Our study focused on *Ficus* species (Moraceae). *Ficus* constitutes one of the most diverse genera of angiosperms with more than 850 species worldwide (Frodin, 2004; Harrison, 2005; Ronsted et al., 2007; Chaudhary et al., 2012; Mabberley, 2017; Mohapatra et al., 2020) and about 124 species in Africa (Berg and Wiebes, 1992; Burrows and Burrows, 2003; Van Noort and Rasplus, 2020; Raji and Downs, 2021). They display a wide range of life strategies, including species that grow as trees, shrubs, Hemi-epiphytes, climbers, epiphyte, free-standing, and creepers. Figs play a keystone role in tropical and subtropical ecosystems globally, basically because of the copious fruit crop they provide, many frugivores consume that throughout the year (Shanahan et al., 2001; Bleher et al., 2003). Although their role has been recorded to be less prominent in some locations (Gautier-Hion and Michaloud, 1989; Peabotuwage et al., 2019), they have been documented to facilitate the seedling recruitment of other neighbouring tree species even in disturbed areas (Caughlin et al., 2012; Cottee-Jones et al., 2016). They are also reported to be important to both insectivorous and frugivores (Matthews et al., 2017; Peabotuwage et al., 2019; Chong et al., 2021).

6.3.2 Camera trap data collection and analyses

We used camera traps to capture fig-frugivore interactions. We placed camera traps at a 1 m range of a fruiting focal *Ficus* tree and focused on identifying the frugivores visiting and

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feeding on fig fruits. The camera traps focused on each focal fig tree for a minimum of three days (Grünewald et al., 2010) and up to 21 days (Ehlers-Smith et al., 2017; Ramos-Robles et al., 2018; Hopson et al., 2020). We placed camera traps at twelve fig trees representing five fig species in four land-use types spread across nine different locations (Tables 6.1 and 6.2) in the urban mosaic landscape of Ethekwini Municipality (Fig. 6.1). The camera traps were a variety of Browning Trail Cameras 900X1600 HD brands, all with night vision capabilities, placed on a 20 s video mode at the highest sensitivity, and ran 24 h/day. The camera traps recorded animals visiting and feeding on fig fruits both day and night as the mammalian frugivores that feed on fig fruits are known to be both diurnal and nocturnal.

We reviewed all of the videos recorded to estimate frugivore visitation and interactions per visit for each focal fig tree, including the number of fruits consumed where detected. We used only videos with frugivore present and identified the level of interaction with the fig plants. We identified frugivores to species level where possible. Some small-bodied and fast birds were not clear enough to be identified, as noted by Quintero et al. (2021) in their research as a limitation for camera trap data. We assigned interactions a score of 1–5 based on the interaction with the focal *Ficus* tree. A score of 1-indicated that an animal was observed in the frame but did not interact with the focal tree and was not close to the fruit, 2- when an animal was observed in the frame, close to the fruit, but did not interact with the fruit. An interaction score of 3- included perching near and examining focal fruit, 4- included pecking at the fruit consuming the seeds or part of the fruits but not whole fruit, and a score of 5 indicated that a frugivore was observed consuming the whole fruit.
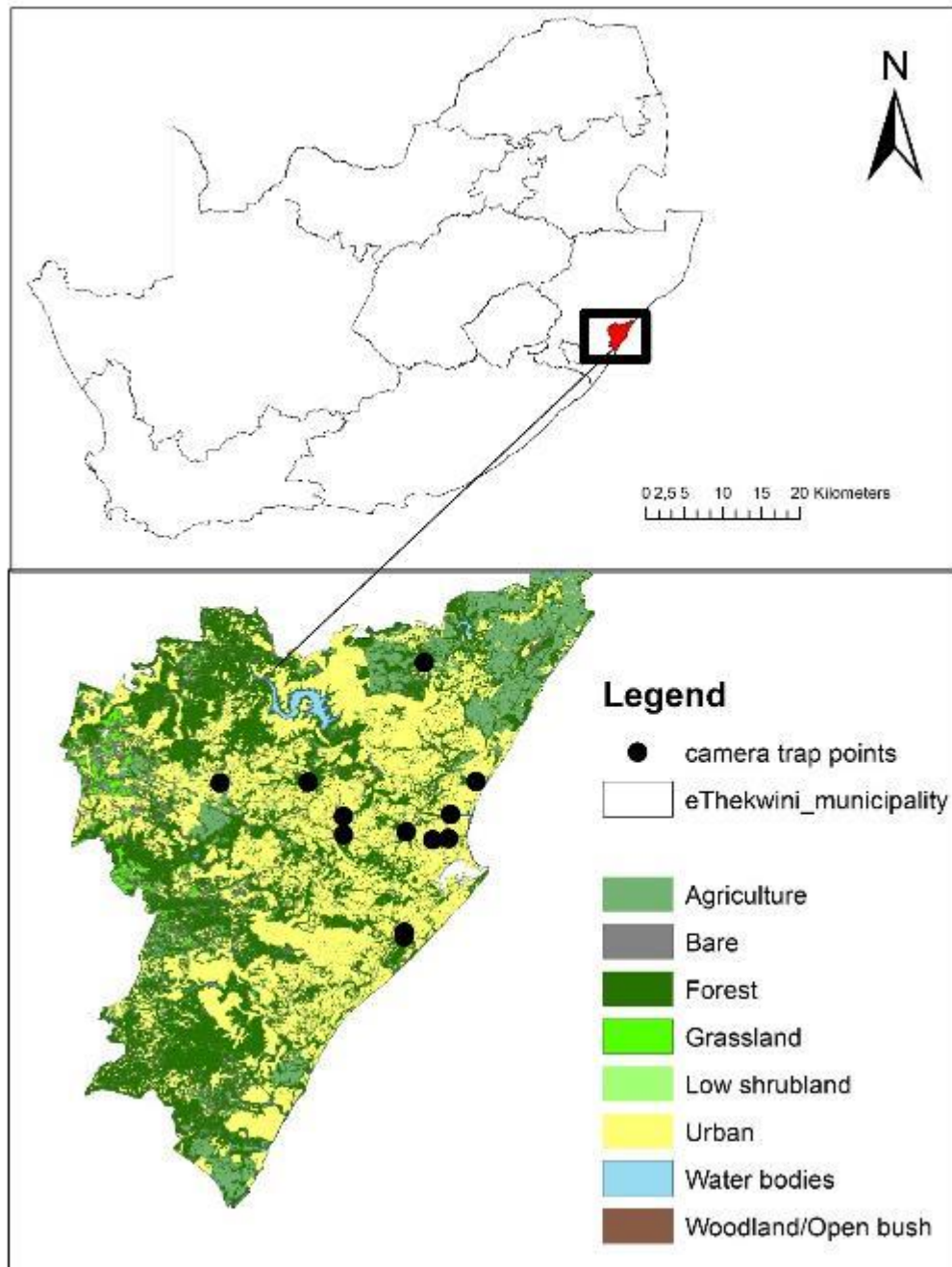
Fig. 6.1. The location of the study area Durban, eThekwini Municipality, KwaZulu-Natal Province, South Africa. The camera trap locations are shown as black dots

To estimate figs fruit-specific total visitation, we included a sum of all interactions with scores of 4 or 5 throughout the sampling period. When we observed interaction with a score of 5, we counted the number of fruits consumed during that visit to calculate the number of fruits

removed. We included all the interactions with a score of (1-5) to estimate fig plants total visitation. The independence of observations was not assured. However, we recorded vertebrate visitation for each video; hence, individual vertebrates might repeatedly be revisiting the same tree for more than 20 s of video records. Therefore, we acknowledge that there might be pseudo-replication of interactions with focal fig trees. However, considering the number of videos recorded of different individuals visiting concurrently, duration of the study and camera trap effort, we consider the interaction data to be indicative of actual patterns. Data were subjected to a visual normality test using the Kolmogorov–Smirnov test and facilitated visually with the use of a histogram. The effect of land-use type and focal fig species on the number of fruit removal per individual visit and visitation rate was analysed using linear (LM) and generalised linear models (GLM). All statistical analyses were done with R statistical software (version 3.6.1, R Core Team, 2018).

6.4 Results

We recorded three main vertebrate frugivorous taxa visiting and feeding on the fig fruits (bats, birds and monkeys). During 3888h, we recorded a total of 4,071 videos from camera traps with 10,016 visits and interactions between these three vertebrate taxa (8958 bat visits, 808 bird visits and 250 monkey visits). These were in five *Ficus* species (*F. burkei*, *F. lutea*, *F. natalensis*, *F. sur* and *F. sycomorus*, Tables 6.1 and 6.2, Supplementary Tables S6.1 and S6.2) across four different land-use types (48 visits in landfill area, 3829 visits in managed green space areas, 4664 visits in nature reserves and 1475 visits in urban built areas) in nine locations (Table 6.1, Supplementary Table S6.1) of the urban mosaic landscape. We also recorded three visits of the large-spotted genet or Cape genet (*Genetta tigrina*), and one visit of a woodland dormouse (*Graphiurus murinus*), interacting with fig trees. Nocturnal activities were

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dominated by fruit bats, with their visits the most abundant and the highest number of fig fruit visits (n = 1255, Table 6.3).

Frugivore interaction with figs was assigned the score of 1-5 as indicated in the methods section. It is worth noting that more than one interaction was observed in some single videos. Given the limitation of some videos' quality, we could not identify some small-bodied and fast bird species. We, therefore, referred to them as unknown birds spp.

The three main vertebrate frugivore taxa recorded differed in their fig fruit feeding behaviour. We observed that birds and vervet monkeys *Chlorocebus pygerythrus* tended to stay for prolonged periods in the *Ficus* trees feeding. In contrast, Wahlberg's epauletted fruit bats *Epomophorus wahlbergi* approached fig trees briefly, then relatively rapidly picked fruits from the trees, and then flew off with these, perhaps to a temporary roosting site. Vervet monkeys spent relatively extended time in the fig trees (>1 min) to process the fruits. They took the whole figs and then either chewed and swallowed the fruits or chewed and spat out the pulp.

Ficus sycomorus attracted the highest number of individual vertebrate visitors (n = 7504, 74.9%, Table 6.2). There was a significant difference among the number of individual vertebrate visits ($F_{2,4729} = 94.5$, $P < 0.0001$) and the number of fruit consumed by the frugivores ($F_{2,4729} = 55.5$, $P < 0.0001$) across the three main vertebrate taxa recorded. There was also a significant difference in the number of visits by the three main vertebrate taxa across the different fig species used in this study ($F_{4,4727} = 15.5$, $P < 0.0001$).

The number of frugivore visits showed a significant difference across land-use types ($P < 0.0001$), and a significant difference between the number of fruits removed by frugivore with land use types ($P < 0.0001$). There was also a significant difference between numbers of vertebrate frugivore visits to different focal fig species ($P < 0.0001$) and numbers of fruits removed by frugivores ($P < 0.0001$).

Table 6.1 Characteristics of figs (Raji and Downs, unpublished data), frugivore visits and fruit removal of the five studied *Ficus* species in the urban mosaic landscape in the present study area. (Note data with an asterisk, Mean ($\pm$ SD) crop size, Mean ($\pm$ SD) persistence of ripening days and Height (m) are from Raji and Downs in prep. Chapter 5)

Species	Common name	Fruiting period	Fruit size (mm diameter)	Fruit colour when ripe	*Mean ($\pm$ SD) crop size	*Mean ($\pm$ SD) persistence of ripening days	*Height (m)	Total vertebrate visits	Sum of fig fruits removed by frugivores
Ficus sur	Broom cluster fig	All year	20-40	Orange-red	24,640 $\pm$ 12800	18 $\pm$ 3	15-25	1383	272
Ficus natalensis	Natal fig	All year	10-20	Reddish-brown	40,000 $\pm$ 7565	14 $\pm$ 3	15-30	738	204
Ficus lutea	Giant-leaved fig	May-January	15-30	Yellowish-brown	22,465 $\pm$ 9419	18 $\pm$ 3	15-25	249	21
Ficus sycomorus	Common cluster fig	All year	20-50	Yellowish-red	20,000 $\pm$ 11082	18 $\pm$ 2	15-35	7504	709
Ficus burkei	Strangler fig, common wild fig	January-October	10-20	Reddish-brown	42,460 $\pm$ 7035	14 $\pm$ 3	15-25	142	49

Table 6.2 Vertebrates visits (Interactions 1, 2, 3, 4 and 5) at each land-use type recorded by camera trap from August 2019- October 2020 in the present study. We also present the fig fruit species they interacted with (Note: FB-*F. burkei*, FL-*F. lutea*, FN-*F. natalensis*, FS-*F.sur* and FSY-*F. sycomorus*).

Frugivores	Land-use types in the urban mosaic landscape				Fig species				
	Landfill	Managed green space	Nature reserve	Urban built areas	FB	FL	FN	FS	FSY
Fruit bats	0	3726	4109	1123	83	99	398	1041	7337
Avian spp.	34	103	393	274	45	150	219	264	126
Monkeys	14	0	158	78	14	0	120	78	38
Genet	0	0	3	0	0	0	1	0	2
Dormouse	0	0	1	0	0	0	0	0	1
Total	48	3829	4664	1475	142	249	738	1383	7504

Table 6.3 Potential vertebrate seed dispersers that visited, pecking on and consumed the fig fruits (Interactions 4 and 5) in each land-use type recorded by camera trap between August 2019 - October 2020 in the present study. We also present the fig fruit species vertebrates interacted with (Note: FB-*F. burkei*, FL-*F. lutea*, FN-*F. natalensis*, FS-*F.sur* and FSY-*F. sycomorus*).

Frugivores	Land-use types in the urban mosaic landscape				Fig species				
	Landfill	Managed green space	Nature reserve	Urban built areas	FB	FL	FN	FS	FSY
Fruit bats	0	711	362	182	15	6	91	167	976
Avian spp.	1	6	158	58	4	19	128	55	17
Monkeys	10	0	32	44	10	0	11	44	21
Total	11	717	552	284	29	25	230	266	1014

6.4.1 Avian species

We identified a total of 32 species of birds visiting and interacting with figs (Supplementary Table S6.2). We recorded 808 visits by birds (Table 6.2). Birds were observed flying through

the frame of the focal spp (interactions 1 and 2), perching (interaction 3), pecking and consuming the figs as whole or parts (interactions 4 and 5). Also, ~15% of the figs were consumed by birds either as whole or parts (Table 6.3). Several bird's species visited multiple fig species (Tables 6.2, 6.3 and Supplementary Table S6.2). Birds were recorded visiting all five species of figs and across the four land-use types of the urban mosaic landscape of the study area (Tables 6.2 and 6.3).

Fig. 6.2. Selected camera-trap photographs of vertebrate frugivores recorded feeding in fruiting *Ficus* tree species in the present study in an urban mosaic landscape of KwaZulu-Natal, South Africa.

6.4.2 Mammalian species

We recorded two main mammalian taxa feeding on fig trees during our studies, the fruit bats and the vervet monkeys. We also had three visits by large-spotted genets and one visit of a woodland dormouse. We recorded a total of 8958 visits by fruit bats and 250 visits by vervet monkeys during the study on four species of figs across the landscape (Table 6.2). Fruit bats have the highest number of visits and fruit consumption across the urban mosaic landscape of the study area (Tables 6.2 and 6.3). *Ficus sycomorus* has the highest consumption (n = 976, 78.1%, Table 6.3.). Of the bat visits recorded, 1255 visits took fig fruits whole (~77% of the figs were consumed by bats) and 86 visits of vervet monkeys were recorded to take whole fruits figs (~9% of the figs were consumed by vervet monkeys), captured in the videos (Table 6.3).

6.5 Discussion

As predicted, we found that several vertebrate taxa visited fruiting *Ficus* tree species in the urban mosaic landscape. In our study, we identified three main vertebrate frugivore taxa, fruit bats, birds and vervet monkeys, as fig visitors and potential seed dispersers of figs fruits. The three frugivore taxa differed in their feeding behaviour. Birds and monkeys tended to stay for prolonged periods (feeding throughout the 20 s video length) on focal trees, whereas fruit bats approached fig trees only briefly, took a fruit, and flew with it perhaps to a temporary dining roost. These feeding behaviour differences may thereby lead to differences in their seed dispersal potential. Previous studies found fruit bats tended to take the fruits to distance, resulting in long-distance dispersal and more scattered seed shadows than birds and monkeys (Handley and Morrison 1991; Korine et al. 2000). Handley and Morrison (1991) and Korine et al. (2000) reported that birds fed in a fig tree for >5 min whereas bats were fast in their approach and took the fruit to roost sites of about 200 m from the focal plants. In our study, an individual fruit bat picked one fruit per visit while small-bodied birds typically pecked on the fruits and

fed on several seeds while the big-bodied birds ingested whole fruits. An individual monkey typically consumed a minimum of three fruits per visit (they either eat or sucked the juice and spat it out).

We also recorded three visits of a large-spotted genet in a *Ficus sur* tree in Umgeni Bird Park (a managed green space land use type). Although we only recorded a perch interaction by the genets, they are a generalist carnivore that includes some vegetative matter in the diet (Widdows and Downs, 2015). They also occur in suburbia in our study area, where they show behavioural plasticity (Widdows and Downs, 2015, 20167, 2018; Widdows et al., 2015). Although not documented in our study, the African civet (*Civettictis civetta*) is reported to feed on figs as part of its diet in South Africa (Amiard et al., 2015). The research also mentioned that they could act as seed dispersers, because of their ability to cover large areas and with long digestion times characteristic of carnivores (Zhou et al., 2008; Amiard et al., 2015).

We observed higher activities at night than in the daytime as more fruit bats visited more than other vertebrate frugivores (birds and monkeys) as predicted. Several factors could be drivers of the visits to and use of fleshy fruited plants in an urban mosaic landscape. These include predator absence, human presence (safety of the frugivores or noise), fruiting phenology, and prolific fruit crops (Korine and Kalko, 2000; Herrera, 2002; Bleher et al., 2003; Daru et al., 2015). Our results showed significant differences between vertebrate visits, fruits removal and fig species. There were also significant differences between the numbers of *Ficus* fruit removed per frugivore visit across the different land-use types.

Ficus tree species typically have year-round fruiting phenology and large crops (Table 6.1, Shanahan et al., 2001; Tang, 2007; Heer et al., 2010). So they provide resources for a variety of vertebrate frugivores that might otherwise be more sparsely distributed (Shanahan et al., 2001; Acipa et al., 2013; Compton and Greef, 2020). This was corroborated in our study. Frugivorous vertebrates typically concentrate their activities where fruit resources are most

visible and abundant. Those fruiting tree species with colourful fruit displays, fruit sizes that can accommodate different vertebrate gapes, high fruit abundance and nutritional content generally attract a greater diversity of frugivorous vertebrates and more frequently (Carlo et al., 2007; Acipa et al., 2013; Compton and Greef, 2020). *Ficus sycomorus* had high frugivore visitation and fruit consumption in our study, which might result from the prolific fruit crops presence on the focal trees.

Frugivores, especially bird species recorded in our study, also used focal trees for perching, which is in corroboration with other studies that fig trees have the ability to offer numerous perching opportunities and food resources for foraging vertebrates may be presumed to be more attractive to frugivorous (Shanahan et al., 2001; Mackay et al., 2018; Compton and Greef, 2020).

Based on our study and others (Shanahan et al., 2001; Eshiamwata et al., 2006; Kuaraksa et al., 212; Kuaraksa and Elliott, 2013; Daru et al., 2015; Mackay et al., 2018), we recommend that fig trees as species for restoration and reforestation programmes. They are highly recommended for conservation programmes in anthropogenically transformed landscapes. We recommend that reforestation programs should give priority to fleshy fruited plant species such as figs that will not only accommodate frugivores but will also attract insectivores and nectarivorous species at the same time serve as perching platform and also be used for nesting, in this case, will not only sustained biodiversity but ultimately ecosystem stability.

6.6 Declarations

Author contributions

Conceptualisation of the study was done by IAR and CTD; methodology, IAR.; data collection, IAR writing—original draft preparation, IAR.; writing—review and editing, CTD. and IAR.;

supervision, CTD.; funding acquisition, CTD and NRF-TWAS. All authors have read and agreed to the published version of the manuscript.

Conflicts of interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, nor interpretation of data; in the writing of the manuscript, nor in the decision to publish the results.

6.7 References

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6.8 Supplementary information

Supplementary Table S6.1. Land-use types and locations of focal fig trees with camera traps in the present study

Land-use types	Locations	*Ficus spp.*
Landfill	Inanda farm (Buffelsdraai)	*F. burkei and F. natalensis*
Managed green space	Umgeni Bird Estuary and area	*F. sycomorus*
Nature reserve	New Germany, Virginia Bush Reserve, Paradise Valley Reserve, and Amanzimtoti Bird Sanctuary	*F. lutea, F. sycomorus, F. burkei and F. natalensis*
Urban built	Commercial areas and residential properties	*F. sur, F. burkei*

Supplementary Table S6.2. The total number of visits by vertebrate frugivores to the five *Ficus* species in the urban mosaic landscape of Ethekwini Municipality, Durban KwaZulu-Natal, South Africa

Frugivores		Total visits to *Ficus* species				
Scientific name		*F. burkei*	*F. lutea*	*F. natalensis*	*F. sur*	*F. sycomorus*
	Common name					
		Avian species				
Muscicapa adusta	African-dusky flycatcher	0	0		0	1	0
Muscicapa caerulescens	Ashy flycatcher	0	3		0	1	0
Lybius torquatus	Black-collard barbet	0	3		0	0	3
Oriolus larvatus	Black-headed oriole	0	0		0	1	0
Spermestes cucullatus	Bronze mannikins	0	0		0	3	0
Cossypha caffra	Cape robin-chat	0	1		0	1	0
Monticola rupestris	Cape-rock thrush	0	0		0	3	0
Zosterops capensis	Cape white-eye	0	4		5	2	0
Streptopelia capicola	Cape-turtle dove	0	0		0	1	0
Trachyphonus vaillantii	Crested barbet	0	0		0	2	0
Pycnonotus tricolor	Dark-capped bulbul	6	3		6	34	5

Species	Common name					
Cercomela familiaris	Familiar chat	0	0	0	1	0
Dicrurus adsimili	Fork-tailed drongo	0	4	0	1	1
Lamprotornis nitens	Glossy starling	0	2	0	0	0
Phoeniculus purpureus	Green wood-hoopoe		2	1		
Bostrychia hagedash	Ibis hadidas	0	0	0	4	0
Spilopelia senegalensis	Laughing dove	0	0	3	4	0
Turdus olivaceus	Olive thrush	0	0	0	20	0
Terpsiphone viridis	African-paradise flycatcher	1	0	0	0	0
Vidua macroura	Pin-tailed whydah	0	0	0	0	25
Tauraco porphyreolopha	Purple-crested turaco	0	1	1	0	0
Streptopelia semitorquata	Red-eye dove	0	1	0	2	0
Onychognathus morio	Red-winged starling	0	1	0	1	3
Psittacula krameri	Rose-ringed parakeet	0	0	0	2	0
Chalcomitra senegalensis	Scarlet-chested sunbird	0	0	0	2	0
Andropadus importunus	Sombre greenbul					
Melaenornis pammelaina	Southern black flycatcher	0	1	0	0	0

Parus niger	Southern black-tit	0	4	0	0	0
Passer diffusus	Southern grey-headed sparrow	3	2	4	1	5
Colius striatus	Speckled mousebird	0	0	0	52	0
Ploceus ocularis	Spectacled weaver	0	0	0	3	1
Serinus gularis	Streaky-headed seed eater	0	0	0	2	0
Ploceus cucullatus	Village weaver	3	0	0	6	23
Crithagra mozambica	Yellow-fronted canary	0	2	0	24	0
	Unknown bird spp	32	178	199	90	60
Mammals						
Epomophorus wahlbergi	Wahlberg's fruit bat	83	99	398	1041	7337
Chlorocebus pygerythrus	Vervet monkey	14	0	120	78	38
Genetta tigrina	Large spotted genet/ Cape genet	0	0	1	0	2
Graphiurus murinus	Woodland dormouse	0	0	0	0	1
	Total Visits	**142**	**249**	**738**	**1383**	**7504**

CHAPTER 7

Summary and Conclusions

"Take care of a fig tree, and you will have figs to eat………… (Proverb 27:18, GNT)"

7.1 Introduction

Numerous studies have shown that anthropogenic land-use change is one of the main drivers of current and future biodiversity loss (Newbold et al. 2013: Zungu et al., 2019). *Ficus* tree species are considered as one of the groups of trees in some forests and across urban mosaic landscapes that provide resources in seasons of general fruit scarcity (Shanahan et al., 2001: Tabarelli & Peres, 2002; Kirika et al., 2008; Albrecht et al., 2017). As a result, various animal species, including avian and mammalian species, have been observed to feed on figs (Shanahan et al., 2001; Cottee-Jones, 2016; Corlett, 2017). They are therefore recognised as playing critical ecological roles, thus contributing to the maintenance of species diversity. Also, some studies have shown that the mutualistic interactions of keystone species such as *Ficus* species can be sensitive to human disturbance. This results in knock-on negative effects that can be long-term on the biodiversity in urban mosaic landscapes and with significant negative consequences to entire frugivore communities (Kirika et al., 2008: Saavedra et al., 2014). However, if populations of *Ficus* tree species can be maintained in anthropogenically modified landscapes, then their mutualistic relationships can persist, and a host of ecosystem services and animal species can be supported (Wilson & Wilson, 2013; Cottee-Jones, 2015). This further offers potential prospects for relatively low-cost forest restoration and maintaining ecosystem function and the strong cultural ties observed between people and *Ficus* trees in several parts of the world (Wilson & Wilson, 2013; Cottee-Jones, 2015). Therefore, it is important to understand the interactions between *Ficus* and vertebrate species and how anthropogenic change in land use affects these interactions to guide conservation and management decisions. Given the above background, this chapter therefore summarises the

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main research findings in relation to the aim and objectives of the present study, involving the following: 1) conducted a systematic review on the distribution and fig-frugivore interactions in Africa; 2) examined the role of ingestion and gut passage by frugivores (fruit bats and birds) on the germination success and seedling emergence of fleshy-fruited *Ficus* species in KwaZulu-Natal, South Africa; 3) determined the presence and fruiting phenology and diversity of *Ficus* species in the urban mosaic landscape of Durban, Ethekwini Municipality, KwaZulu-Natal, South Africa and finally, 4) determined the foraging behaviour and visitation of vertebrate taxa to fruiting *Ficus* tree species in this urban mosaic landscape of Durban.

7.2 Findings and discussion

Anthropogenic land-use changes can have intense effects on the interaction between fleshy fruited plants and frugivores, and by extension, all those species that rely on these seed dispersers (Rodríguez-Estrella, 2007; Makau, 2016). It is predicted that by 2030, southern Africa might experience the largest increase in urban land in areas with high biodiversity (Güneralp & Seto, 2013; Zungu et al., 2019). Of the 70 eligible papers reviewed in this study (Chapter 2), which included the web search for frugivore-fig interactions and *Ficus* distribution in Africa, a total of 124 *Ficus* species were recorded across 30 African countries representing approximately 56% of the African countries (Chapter 2). Cameroon had the highest record of 63 species, while Benin, Burundi, Ghana, and Rwanda had two, the least number of *Ficus* spp. recorded (Chapter 2). East Africa had the highest *Ficus* spp. richness recorded (96 species), followed by southern Africa (74 species), Central and Northern Africa (72 species), and West Africa with the least (31 species) recorded (Chapter 2).

Fruit-frugivore interactions are mutually beneficial, with fruit handling behaviour of frugivores playing a key role in determining their contribution to the seed dispersal process and plant recruitment (Jordano & Schupp 2000; Wilson & Downs, 2012; Crestani et al., 2019).

These include but are not limited to transportation of seeds away from parent plants (seed dispersal), forest regeneration and biodiversity maintenance (Fenner & Thompson; 2005; Jordaan et al. 2012; Kitamura 2011; Caughlin et al. 2013; Shikang et al., 2015). These interactions may also increase or decrease germination probability after seeds have passed through frugivore's guts and reduce seed germination time (i.e. seedling emergence) after consumption (Traveset & Verdú 2002, Samuels & Levey 2005; Pires et al., 2018). Therefore, in Chapters three and four, the role of avian frugivore species and fruit bats contribution to *Ficus* plant recruitment were investigated by testing the effects of fleshy fruited fig seed gut passage and ingestion on seed germination success and seedling emergence. *Ficus* fruits were fed to captive avian frugivores and fruits bats. Ingested seeds were collected from excreta or faecal droppings and spat seeds, then planted and their germination responses in terms of seedling emergence and germination success determined. These were compared with the germination responses of manually depulped and whole fruits of figs planted at the same time and under similar conditions. Seedling emergence and germination typically increased for *Ficus* seeds ingested by birds and fruit bats compared with de-pulped and whole fruits (Chapters 3 and 4). This, also concurred with previous studies, showing the importance of frugivorous bird and fruit bat species in potential seed dispersal and germination success (Shanahan et al., 2001; Muscarella & Fleming 2007; Tang et al., 2007; Heer et al., 2010; Jordaan et al., 2012; Rollinson 2013; Kunz et al., 2011; Pulzatto et al., 2018; Amponsah-Mensah et al., 2019).

In Chapter five of this study, the distribution of *Ficus* tree species, their diversity and fruiting phenology in the urban-forest mosaic landscape of eThekwini Municipalitywas examined. It was predicted that more *Ficus* tree species were in the forest areas and that *Ficus* fruiting occurred throughout the year. However, the result showed that the urban built areas had the highest number (128) of fig trees, and most of the fig trees in the nature reserves were

recorded along the forest edges, with relatively few figs inside the forests. In addition, the highest number of fig species were recorded in the urban built areas (n = 7 species) and nature reserves (n = 7 species). Information gathered from citizen scientists revealed that some of the fig trees in the urban built area were planted. Seven species and 478 individual fig trees in the urban-forest mosaic landscape of eThekwini Municipality. These included (a) *Ficus natalensis,* (b) *F. lutea,* (c) *F. sycomorus,* (d) *F. tricopoda,* (e) *F. polita,* (f) *F. sur* and (g) *F. burkei.* The most abundant fig tree species recorded across all land-use types were *F. natalensis* (124 stems, 26%), followed by *F. tricopoda* (110 stems, 23%) while *F. sur* (31 stems, 7%) was the least abundant. The ripening persistence of *Ficus* fruits ranged from 14-20 days (Chapter 5). According to our observations and data collected (Chapter 5), fruit-ripening persistence depended on fruit sizes. Fruits of *F. natalensis*, *F. burkei,* and *F. tricopoda* with relatively smaller fruit sizes took an average of two weeks to ripen ($\pm$ 14 days, Chapter 5), while other species with larger fruit size had a longer ripening time.

Importantly *Ficus* fruits were available throughout the 18 months of the sampling in the urban mosaic landscape (Chapter 5). Although, F. *lutea* and *F. tricopoda* were not fruiting between February-April, the other species *F. natalensis*, *F. sur,* and *F. sycomorus* had fruits throughout the year (Chapter 5) and not all individual trees were fruiting simultaneously. The total number of fig fruits available (crop size) recorded varied between 1780 and 48550 per monitored tree (Chapter 5).

Lastly, vertebrate frugivore visits to fruiting *Ficus* tree species in the urban mosaic landscape was determined using camera traps videoing fig-frugivore interactions (Chapter 6). All the videos were reviewed to recorded to estimate frugivore visitation and interaction per visit for each focal fig tree, including the number of fruits consumed. A total of 4,071 videos of camera trapping with 10,016 visits and interactions between three vertebrate taxa (8958 fruit bat visits, 808 bird visits and 250 monkey visits), and five *Ficus* species (*F. burkei*, *F. lutea*,

F. natalensis, *F.sur* and *F. sycomorus*, Chapter 6) across four different land-use types were recorded. *Ficus sycomorus* attracted the highest number of individual visitors (n = 7504). Nocturnal fruit bat visits were the most highest in terms of total visitation and also the highest with respect to the number of fig fruits visits (n = 1255, Chapter 6). There were significant relationships between vertebrate visits, fruits removal and fig species. There was also significant relationships between the number of fruit removal per frugivore visits across different land-use types. Due to the prolific and year-round fruiting of *Ficus* tree speciess, they are considered important species for the regeneration of plant communities and persistentence of vertebrate frugivorous taxa as found in other studies (Galindo-Gonzalez et al., 2000; Holl et al., 2000; Schlawin & Zahawi, 2008; Corbin & Holl, 2012; Cottee-Jones et al., 2016). The results presented in this study are of value in the management and conservation of these food resources and their dependant vertebrates in urban mosaic landscapes.

7.3 Implication for conservation

The phenological patterns of *Ficus* tree species in the study area showed that their fruits were available all year round, implying that there are important to frugivores, especially during food scarcity. In a mutual relationship, frugivores enhance germination rates and the emergence of *Ficus* seedlings. Frugivores gut passage of *Ficus* seeds improved germination and seedling establishment. Consequently, beyond the transportation of seeds away from the mother plant, vertebrate frugivores generally play a major role in *Ficus* recruitment. They also typically cover a relatively large area and long distances for foraging so enhance gene flow between populations from different habitat fragments (Bernard & Fenton 2002; Heer et al., 2010; Trevelin et al., 2013; Pulzatto et al., 2018). This highlights the importance of *Ficus* seed ingestion by avian and fruit bat species for the restoration of degraded areas enhancing conservation.

7.4 Conclusions and recommendations

Native trees are fast disappearing as a result of a change in land uses, such as agricultural, and a result of the human-modified landscapes, particularly in Africa (Tilman et al., 2017). These anthropogenic and-use changes result in various ecological consequences including the genetic isolation of frugivore populations in forest fragments, and a reduction in seed dispersal and regeneration potential in non-forest habitats, leading to a local extirpation of fleshy fruited trees (Bleher et al., 2003; Caves et al., 2013; Cottee-Jones, 2014). Some of the fig trees in the urban area of this study were planted. This suggests that planting *Ficus* tree species could be an important management tool to sustain the diversity of frugivorous animals in an urban mosaic landscape. The asynchronous ripening pattern and copious crops of *Ficus* species recorded and observed in the present study suggest a "steady state" availability of fruits for some species of figs over a long period (14-20 days) and all year round. These fruiting cycles make them important food resources and attractive to wide range of frugivores. For example, individuals of *F. natalensis*, *F. sur,* and *F. syncomorus* fruited each month of the study. In addition to the fruiting availability of *Ficus*, studies have shown that their fruit contains a range of essential nutrients and minerals (O'Brien et al., 1998; Korine et al., 2000; Shanahan et al., 2001; Acipa et al., 2013; Compton & Greef, 2020). The fruits of *Ficus* species recorded in the present study were also of different colours, fruit sizes with large and rewarding fruit crops (Chapter 5). This showed that they are vital in supporting diverse groups of frugivores (e.g., fruit bats, birds and primates, Chapter 6).

Consequently, conservation and management programmes that will enhance the conservation of *Ficus* tree species and conserve the range of vertebrate frugivores that depend on their fruits must be put in place, particularly in Africa where changing land use continues with increasing human populations. Further research is required on the role that *Ficus* species play in regenerating economically and medicinally valuable plant resources in rural and

periurban areas of Africa. In addition, the impacts of anthropogenic land-use changes on *Ficus* tree species populations and the adverse impacts of their demise on frugivore persistence, both in natural forests under high human pressures and in the urban mosaic landscape areas of Africa are needed. Planting of keystone *Ficus* tree species for restoration projects will act as a seed bank reducing the cost involved in seed collection because of their ability to produce large fruit crops all year round. They also serve as habitat corridors and enhance landscape connectivity for plants and frugivores, accelerating the recovery of degraded landscapes. *Ficus* tree species planted in urban areas for urban greening will also attract certain frugivore species that depend on their fruit, especially in periods of food scarcity.

7.5 References

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