

**RESPONSE OF BIRD ASSEMBLAGES TO THE INVASION AND CLEARING OF
ALIEN TREES IN THE WESTERN CAPE, SOUTH AFRICA**

by

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Thesis submitted in fulfilment of the requirements for the degree

Master of Technology: Conservation and Marine Sciences

in the Faculty of Applied Sciences

at the Cape Peninsula University of Technology

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Cape Town
November 2016

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ABSTRACT

Invasive alien plant species pose a major threat to global biodiversity by displacing native vegetation and transforming habitats. In South Africa, invasive alien plants have become a major component of most habitats. River systems are particularly affected owing to their dynamic nature and to anthropogenic activities. This has resulted in fynbos riparian scrub vegetation being replaced mainly by *Acacia* and *Eucalyptus* species, with serious ecological and economic impacts. The presence of alien trees along river banks leads to a reduction in native plant species richness and their high water consumption adds on to the existing water challenges in an already dry country. However, with regards to native fauna, it largely remains unknown both at small or large spatial scale, whether alien trees provide additional habitat which increases biodiversity, or if their presence leads to a reduction of native biodiversity. Impacts on water supply have led to large-scale clearing of invasive alien trees from riparian zones by the government through the Working for Water (WfW) programme. Monitoring and evaluation studies carried out after clearing are not well-rounded and mostly focus on vegetation response to clearing. Although some of these studies have reported successful restoration through passive methods, ecosystem recovery remains partial. There is evidently a lack of information regarding the response of animal communities to invasive alien plant clearing. Therefore, the main objective of this thesis was to investigate bird assemblage response to alien tree invasion and clearing.

As a study system, I used the riparian area of the Berg River within the fynbos biome of the Cape Floristic Region, South Africa. The area historically consisted of renosterveld vegetation characterised by a matrix of shrubs and a high diversity of geophytes but relatively poor avifaunal diversity. This area is heavily affected by invasive alien trees and shrubs including *Eucalyptus camaldulensis*. I employed bird assemblages as an indicator, and used fixed-point bird counts to compare bird species richness and bird abundance between invaded and near-pristine habitats. Invasion by *E. camaldulensis* significantly reduced bird species richness and abundance. In particular, nectarivores and frugivores, which play important mutualistic roles in the fynbos, were reduced and unexpectedly; there were fewer raptors in invaded areas.

I proceeded to carry out a space for time substitution, comparing plant and bird assemblages in invaded sites, near-pristine sites and in sites cleared in 2005, 2007, 2008 and 2014. A general increase in bird species richness and bird abundance with time since clearing exists with bird assemblages in cleared sites being similar to those in near-pristine sites. However, bird assemblages in cleared sites have not yet fully recovered a decade after clearing and four native

plant species are still absent. In the third part of my thesis I assessed the impacts of invasive alien plants on bird assemblages at a larger spatial scale. The different responses shown by bird assemblages to invasive alien plant cover depended on the intensity of invasion, spatial scale and other land uses.

From a bird's eye view, this study supports the current clearing by WfW given the significant negative effects of invasive alien plants on bird diversity both at plot and large spatial scales. However, passive restoration is unsuccessful in restoring the full complement of plants and birds, therefore, active restoration should be considered. To limit the cost, I suggest a focused restoration approach of selected keystone tree species which can assist to establish a functional native ecosystem.

ACKNOWLEDGEMENTS

I would like to give gratitude to God the Almighty for the opportunity to study and for seeing me through, may all glory and honour be to Him. You showed me that even in hard times I can still get “the peace of God which surpasseth all understanding... through Jesus Christ” (Philippians 4: 7).

I would also want to express a heartfelt gratitude to the following people and organisations:

- Dr. Sjikr Geerts (my main supervisor) for the great help, invaluable support, guidance, ideas, as well as consistent patience and encouragement
- Dr. Mirijam Gaertner and Prof. Joseph I. Kioko (my co-supervisors) for guidance, input and correction of my drafts
- The financial assistance of the National Research Foundation towards this research is acknowledged. Opinions expressed in this thesis and the conclusions arrived at, are those of the author, and are not necessarily to be attributed to the National Research Foundation.
- The DST-NRF Centre of Excellence for Invasion Biology and the Working for Water Programme through their collaborative research project on “Integrated Management of invasive alien species in South Africa” for additional funding
- Jacobus Mullers for help with geographical information systems
- ADU for SABAP2 data
- Prof. van Schalkwyk for statistical guidance
- Dr. Lynn Nemaramba-Mafofo for language editing
- The landowners around the upper Berg River catchment who allowed access to their properties
- Dr. Farai Tererai for site location assistance
- Michelle Slabber and Richardt Smith for fieldwork assistance
- Nyasha Magadzire for general assistance
- My husband Aaron and daughter Atida Pearl for the patience throughout the study period
- All the baby sitters, Sharon, Patience and Tapiwa, the Magadzires, the Mushandus, the Mudares and Petronella. Thanks for putting my mind at rest when I was away at conferences and for a sleepover in the lab.
- My mums and the girls for the prayers
- All the girls in lab 3.43, you made the days shorter.

DEDICATION

Always for the girls.

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CHAPTER ONE GENERAL INTRODUCTION

1.1. Introduction and impacts of invasive alien plants

The recent increase in human migration, owing to transport innovations and international trade, enabled the transportation of biological material across traditionally existing natural barriers (McNeely 2006; Hulme 2009). The rise in human mobility facilitated the transportation of thousands of plant species around the globe (Hulme 2009). Some of the introduced alien plants naturalised and subsequently invaded the recipient ecosystems with impacts on biological diversity, ecosystem functions and services (Vilà *et al.* 2011; Pyšek *et al.* 2010).

The impacts of invasive alien plants differ depending on invading plant species, the extent of invasion and the vulnerability of the ecosystem being invaded (van Wilgen *et al.* 2001; Richardson & van Wilgen 2004). Existing evidence also shows that effects on native plants spill-over and affect resident animal communities with specialised species eventually being displaced (French & Major 2001; Samways & Taylor 2004; Tallamy 2004). Impacts on wildlife occur directly via a decrease in available food; even for higher-trophic feeders such as birds (Holland-Clift *et al.* 2011). These impacts result in invasion by alien plants to be the second largest global threat to biological conservation, after direct habitat loss (Wilcove *et al.* 1998; Pimentel *et al.* 2001).

According to van Wilgen *et al.* (2001), plant species from other parts of the world have been introduced into South Africa for a range of purposes including food provision, timber, firewood, garden ornamentals, stabilizing sand dunes and as barrier and hedge plants. By 2010, approximately 8750 plant species had been introduced into South Africa with 660 plant species being listed as naturalised species (Wilson *et al.* 2013). Out of the naturalised species, 379 plant species are recognised as invaders in the National Environmental Management: Biodiversity Act 2004 (Act 10 of 2004) Draft Alien and Invasive Species List of 2014 (Department of Environmental Affairs (DEA), 2014). According to Binns *et al.* (2001) and Henderson (2007), most natural and semi-natural areas which make up more than 10 million ha or 8% of the country's total surface area, have been affected by invasive alien plant species. Goldblatt & Manning (2012) suggest that a serious problem is presented in the Cape Floristic Region (CFR), which contains the fynbos biome. The CFR is species-rich with over 9000 plant species and about 6300 of these plant species are endemic (Goldblatt & Manning 2012). Binns *et al.* (2001) also note that this high level of endemism is under threat because in addition to impacts from urbanisation and farming, the presence of invasive woody alien plants in this region has

displaced 36% of fynbos ecosystems (Higgins *et al.* 1999). The further existence of remaining species is greatly endangered (Binns *et al.* 2001).

Tree invasions have recently become a huge concern in treeless areas such as the fynbos shrublands (Rundel *et al.* 2014). Several characteristics of alien trees, including the ability to extract large amounts of water and nutrients (van Wyk 1987, Le Maitre *et al.* 1996), the ability to alter fire ecology and soil physico-chemical properties (Yelenik *et al.* 2004; van Wilgen *et al.* 2012), and the absence of natural regulators such as herbivores and disease (Keane & Crawley 2002; Colautti *et al.* 2004) gives alien trees a competitive advantage over native plant species. In the fynbos, a number of forestry plantation species including *Acacia*, *Pinus* and *Eucalyptus* have become invasive with negative impacts far beyond forestry areas (Le Maitre *et al.* 2000; Mondlane *et al.* 2001; Forsyth *et al.* 2004). The resulting altered vegetation communities present direct negative impacts on faunal communities through changes in the availability of primary resources such as suitable habitat, food and breeding sites (Samways *et al.* 1996; Samways & Taylor 2004; Dean *et al.* 2002; Procheş *et al.* 2008). Bird assemblages have been particularly affected by invasion, resulting in a decrease in species richness of some specialist foragers such as nectarivores and frugivores and consequently the disruption of pollination and seed dispersal (Fraser & Crowe 1990; Greve *et al.* 2011; Rogers & Chown 2013). Furthermore, the disruption of these mutualistic plant-animal interactions affects the perpetuation of natural communities and subsequently ecosystem structure and functions (Traveset & Richardson 2005). With such numerous impacts from tree invasions, the need to control them becomes justified (van Wilgen *et al.* 1998; 2012).

1.2. Invasion and restoration of riparian zones

According to Hood and Naiman (2000), riparian zones provide linear habitats that cover a relatively small surface area of the landscape whilst at the same time supporting highly diverse plant and animal communities. This is due to natural processes, such as flooding, that enable the efficient transportation and deposition of propagules as well as the maintenance of consistently high levels of moisture and nutrients (Planty-Tabacchi *et al.* 1996; Naiman & Décamps 1997; Hood & Naiman 2000; Nilsson & Berrgren 2000). In addition, disturbances occurring in rivers through human use (e.g. crop cultivation, damming and irrigation) create gaps and opportunities for colonisation by plants (Hood & Naiman 2000; Nilsson & Berrgren 2000; Glenn & Nagler 2004). Also because they are a boundary between aquatic and terrestrial ecosystems, riparian zones perform several ecological functions such as moderating local environmental conditions through the control of moisture (Naiman & Décamps 1997; Hood & Naiman 2000). This leads to a distinct habitat for plants and animals in these areas (Naiman &

Décamps 1997; Hood & Naiman 2000). However, riparian habitats are susceptible to invasion by alien plants due to the same factors that support their high biodiversity (Planty-Tabacchi *et al.* 1996; Richardson *et al.* 2007; Shaffroth & Briggs 2008).

South Africa's riparian areas have not been spared from invasion by alien plants with most river systems, particularly in the CFR, being extensively affected and highly transformed (Mondlane *et al.* 2001; van Wilgen *et al.* 2001; Forsyth *et al.* 2004). Species in the genera *Acacia*, *Hakea* and *Pinus* make up the bulk of invasive plant species in the Cape Floristic Region (Richardson and van Wilgen 2004). *Eucalyptus camaldulensis* is also abundant in most riparian areas (van Wilgen 2009, Dzikiti *et al.* 2016). In a rapid assessment, Forsyth *et al.* (2004), notes that 46% of rivers in the Cape Floristic Region, are invaded by *E. camaldulensis*. Generally, eucalypts are known to compete with indigenous plants for resources such as water and light (Thorburn *et al.* 1993). Their presence also impedes the germination and establishment of indigenous riparian plants through the accumulation of a thick litter layer and through allelopathy (Bernhard-Reversat 1999, Sasikumar *et al.* 2001). This leads to *Eucalyptus* dominated riparian forests that lack the undergrowth typically associated with riparian habitats (Ruwanza *et al.* 2013a, b; Dzikiti *et al.* 2016; pers. obs.). Although evidence of impacts on plant communities is available, impacts of *E. camaldulensis* on animal communities in riparian areas remain largely unexplored. There is no evidence showing whether the occurrence of *E. camaldulensis* in riparian and terrestrial areas complement or reduce existing habitats. Nonetheless the effects of invasive alien trees; and not just of eucalypts; on riparian vegetation have been acknowledged to proliferate to and negatively affect higher-level consumers such as birds through a loss or decline of foraging substrates and nesting sites (Dean *et al.* 2002).

The numerous impacts of invasive tree plant species on ecosystem services, such as water supply and biodiversity conservation, led to the initiation of a government sponsored invasive alien plant clearing programme, Working for Water (WfW) (van Wilgen *et al.* 1998; Esler *et al.* 2008). WfW also clears alien plants from terrestrial ecosystems, but their primary objective is to clear alien plants from watersheds to secure water resources in a predominantly dry country (van Wilgen *et al.* 1998; 2012; Esler *et al.* 2008). Although their efforts are also intended at assisting ecosystem recovery, the risks and expenses associated with ecological restoration makes WfW reluctant to commit (Crokes *et al.* 2013), despite the ecological gains that can be realised (de Wit *et al.* 2012). Since its inception, WfW has been working under the assumption that cleared ecosystems recover in structure and function and consequently, regain resilience without further assistance (Esler *et al.* 2008; Holmes *et al.* 2008). They employ a passive

approach, removing the invader from riparian areas and conducting follow-up clearing to reduce remaining propagules (Galatowitsch & Richardson 2005).

Working for Water (WfW) generally relies on passive restoration to initiate post-disturbance plant succession and also to re-establish lost native plant communities (Galatowitsch & Richardson 2005; Esler *et al.* 2008). In riparian systems, areas that are found higher up in the catchment are relatively intact and naturally re-establish (Prins *et al.* 2004; Blanchard & Holmes 2008). Autogenic recovery occurs through several ways, including reproduction by surviving native plants, resprouting from plant structures in the soil, from native soil-stored seedbanks and also through seed dispersal (Roberts & Gilliam 2003; Impson *et al.* 2013). In highly degraded areas including foothill and downstream sections, restoration may be successful through passive methods but mostly fails when biotic (e.g. changes in species richness and soil seed banks) and abiotic (e.g. changes in soil physico-chemical properties) thresholds have been crossed and ecosystem resilience has been lost (Prins *et al.* 2004; Gaertner *et al.* 2012). In other instances, the threat of secondary invasions also limits the success of passive restoration (Galatowitsch & Richardson 2005; Beater *et al.* 2008; Ruwanza *et al.* 2013 a, b). Where passive restoration is unsuccessful, additional restoration activities such as employing mechanisms to improve the soil's physico-chemical properties and/or introducing native plants after removing the invader are required to assist ecosystem recovery (Hobbs & Norton 1996; Holmes *et al.* 2005). Monitoring activities post-clearing are important to ascertain restoration success (Kentula 2000; Heleno *et al.* 2010). However, WfW rarely carries out monitoring activities post-clearing to evaluate if recovery of cleared areas has occurred (Beater *et al.* 2008).

1.3. Measuring restoration success in cleared riparian areas

A major obstacle of the ecological restoration process is the definition of a reliable measure of success (Longcore 2003; Wood 2011). This is because determining the measure of success for restoration projects can be complex (Fletcher *et al.* 2007; Hobbs 2007). Ecological restoration projects may be evaluated using a reference site (Hobbs 2007) and success can be described as improved ecosystem functions and/or services and ecosystem resilience (Kentula 2005; Wood 2011; Gaertner *et al.* 2012). The majority of studies assessing ecosystem restoration success following alien tree clearing focus on native vegetation recovery (see Galatowitsch & Richardson 2005; Beater *et al.* 2008; Morris *et al.* 2008; Ruwanza *et al.* 2013a, b). However, evaluation should also focus on the recovery of faunal assemblages (Heleno *et al.* 2010; Atkinson *et al.* 2015). It has only been recently that the response of fauna in restored ecosystems has begun to receive more attention (e.g. Heleno *et al.* 2010; Magoba & Samways 2010; Samways *et al.* 2011; Shanahan *et al.* 2011; Atkinson *et al.* 2015). Birds have been found

to be useful biological indicators in this respect, because they are ecologically versatile and can be monitored relatively inexpensively, are highly mobile and react rapidly to changes in their habitat (Dobson *et al.* 1997; Burnett *et al.* 2005). Compared to other groups of organisms, birds are generally well known, reasonably easy to identify and are well diversified and feed at different trophic levels (Dobson *et al.* 1997). Bird communities are largely determined by the availability of suitable habitat (Lindenmeyer *et al.* 2002). Thus, changes in bird assemblages can be used to monitor the effectiveness of restoration efforts and interpret restoration success.

1.4. Research aims and objectives

The aims of this study were firstly to investigate whether *Eucalyptus camaldulensis* invasion in the riparian area of the Berg River, Western Cape, South Africa affect faunal communities. It is generally acknowledged that invasive alien trees affect vegetation communities and therefore often present a basis to argue for invasive tree clearing (Le Maitre *et al.* 2011; Tererai *et al.* 2013). However, impacts on faunal communities are less well understood (Samways *et al.* 1996). This study addresses this gap by investigating impacts of tree invasion in riparian forests with the focus on bird assemblages.

Secondly, clearing of invasive trees is currently taking place in many riparian areas in South Africa. It is imperative that the monitoring of cleared areas is carried out in order to ascertain success and justify the need to continue funding invasive alien plant clearing. Most studies concentrate on the response of plant assemblages following clearing with no insight on the recovery of other taxa (Atkinson *et al.* 2015). This study fills this breach in knowledge by assessing whether avifauna displaced by plant invasions successfully re-establishes post clearing.

This study is the first to evaluate the effects of alien invasive tree clearing in riparian areas of the fynbos biome using bird assemblages. In addition, the study explores whether the same trends shown by birds at the plot scale in a *Eucalyptus* invaded riparian ecosystem manifests on a larger scale.

In order to address these aims, the following specific objectives were used:

- To ascertain the use of invaded and native vegetation riparian habitats by different bird feeding guilds.
- To assess the effect of post clearing vegetation recovery on bird populations in passively restored areas.

- To use bird assemblages to suggest a list of keystone plant species for active introduction.
- To assess bird assemblages' response to invasive alien plant cover at different spatial scales.

1.5. Thesis outline

Chapter one: General Introduction

This chapter provides a general introduction on invasion, impacts of invasion, management of invasive alien plants and the need for measuring restoration success with focus on the Cape Floristic Region (CFR). Also included in this chapter are the aims and objectives of the study.

Chapter two: Alien invasive trees reduce bird species richness of mutualistic frugivores and nectarivores; a bird's eye view on a conflict of interest tree species in riparian habitats.

In this chapter I assess the impacts of *Eucalyptus camaldulensis* invasion in riparian zones on faunal communities. It is not clear if alien trees in riparian areas provide important habitat for wildlife or if their presence affect biodiversity. I compare bird assemblages in invaded and near-pristine habitats of the Berg River, South Africa and used the results to support the current clearing of invasive alien plants from affected systems.

Chapter three: Bird and plant assemblages' recovery following removal of an alien tree invader from the riparian habitat of the Berg River, South Africa.

I use a chronosequence approach to assess whether vegetation and bird assemblages recover following the removal of *Eucalyptus camaldulensis*. I assess vegetation and bird assemblages in cleared sites, while assemblages in invaded and uninvaded sites serve as a reference. I then hone in on the importance of bird assemblages as a guide to restoration.

Chapter four: It is all about land use: bird assemblages' response to invasive alien plant cover at different spatial scales.

Here I expand on the work from chapter 2, testing whether the effects of invasion on bird assemblages show consistent patterns at larger spatial scales. I employ geographical information systems to show the impacts of alien trees on bird assemblages in the CFR.

Chapter five: Conclusions and recommendations

Here I provide an overview of the results, highlight the new contributions and point to potential future research opportunities.

Chapter 2 and 3 are written aimed for submission to different journals and have more than one author hence the use of “we”. The student (J.R. Mangachena) is the first author in all chapters and had the main responsibility for designing the study, field work, data collection, data analysis and manuscript writing while the supervisors helped with conceptualising ideas, planning and commenting on manuscript drafts.

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CHAPTER TWO

INVASIVE ALIEN TREES REDUCE BIRD SPECIES RICHNESS AND ABUNDANCE OF MUTUALISTIC FRUGIVORES AND NECTARIVORES; A BIRD'S EYE VIEW ON A CONFLICT OF INTEREST SPECIES IN RIPARIAN HABITATS

Abstract

Invasive alien plants have major ecological impacts and riparian habitats are particularly prone to plant invasions. While impacts of alien tree invasions on riparian plants are well studied, impacts on animals are not well understood. Invasive alien trees can have a positive effect by adding habitat and food sources, or have a negative effect, by replacing native food plants. Here we use birds as indicators to determine the impacts of *Eucalyptus* tree invasion in riparian areas of South Africa. Birds are an ideal study group because they are mobile, respond quickly to habitat changes and feed at different trophic levels. Fixed-point bird counts were done during winter and spring at near-pristine and *Eucalyptus camaldulensis* invaded habitats. A total of 1142 birds from 44 species were recorded. Bird assemblages in invaded sites are almost a complete subset (24 species) of those in near-pristine areas (42 species). Invaded sites had significantly lower bird species richness and abundance as 128 birds from 18 species are lost. This decline is largely due to fewer frugivores and a total absence of nectarivores. In strong contrast to previous reports, we found fewer raptors in invaded areas. From a bird's perspective, the current large scale removal of *E. camaldulensis* from South Africa's river systems is justified, but whether the full complement of bird species of the near-pristine site will return to cleared areas still needs to be determined.

Key words: Bird feeding guilds; Cape Floristic Region; *Eucalyptus camaldulensis*; Nectar feeding birds; Plant invasions; Raptor.

2.1. Introduction

Riparian systems comprise only a small fraction of the landscape, but support a rich and distinct plant and animal communities (Naiman & Decamps 1997; Robinson *et al.* 2002; Jacquemyn *et al.* 2010). Riparian areas can be disproportionately rich in plant species due to consistently high levels of moisture and nutrients and regular flooding episodes, which result in high propagule transportation (Planty-Tabacchi *et al.* 1996; Naiman & Decamps 1997). Due to this high plant species richness, riparian areas as well as important habitats and movement corridors for fauna in highly transformed landscapes (Robinson *et al.* 2002). However, riparian zones are also more susceptible to invasion by alien plants due to the same factors that support this high species diversity (Planty-Tabacchi *et al.* 1996). Consequently riparian areas are some of the most invaded systems globally (Richardson *et al.* 2007).

Alien plant invasions in riparian areas displace native vegetation, changing the vegetation structure and floristic composition (Hejda & Pyšek 2006; Schwartz *et al.* 2006; Hejda *et al.* 2009, Tererai *et al.* 2013). Although impacts on plant communities are relatively well studied, this is not the case for animals (Samways *et al.* 1996). However, the few studies available show that impacts on the flora do translate into impacts on animals. For example, invasive alien species can lead to a reduction in riparian herbivorous insect populations (Greenwood *et al.* 2004; Gerber *et al.* 2008). Decline in insect populations may directly affect higher-trophic feeders such as birds through a decrease of primary food resources (Procheş *et al.* 2008). Furthermore, the displacement of native riparian vegetation by invasive woody plants simplifies habitat structure which results in a reduction of breeding and nesting sites for bird assemblages (Simberloff *et al.* 2010; Holland-Clift *et al.* 2011).

Birds are an ideal taxon to study the impacts of invasive alien vegetation. Firstly, they are mobile and easy to identify; secondly, they feed at higher trophic levels and thirdly, they respond quickly to changes in vegetation structure and plant composition (Dobson *et al.* 1997; Burnett *et al.* 2005). Several studies which previously explored the impact of invasive alien plants on bird assemblages reported negative impacts (e.g. Dean *et al.* 2002; Greve *et al.* 2002; Holland-Clift *et al.* 2011), positive effects (Le Roux *et al.* 2010, Geerts & Pauw 2013; Rogers & Chown 2013) or no effects (Shanahan *et al.* 2011). Thus, bird assemblages' response to invasive alien plant species depends on the bird species in question, the invading alien plant species and the affected ecosystem (Fraser & Crowe 1990; Sogge *et al.* 2008). In most cases, responses of bird assemblages to habitat changes are linked to their specialization on certain food resources (Grass *et al.* 2013). For instance, thicket-forming invasive alien plants may become barriers to insectivores hunting for aerial insects (Avarind *et al.* 2010) whilst changes in plant species composition may render a habitat unsuitable for nectarivores (Grass *et al.* 2013). In contrast, certain insectivores and mixed feeders increased in abundance in sites dominated by invasive alien *Acacia* (Rogers & Chown 2013). Similarly, granivores and insectivores increased in response to *Acacia*, *Eucalyptus* and *Pinus* invasions (Fraser & Crowe 1990). The presence of fleshy-fruit bearing invasive plants such as *Lantana camara*, *Solanum mauritanium* and *Cinnamomum camphora* leads to an increase in the abundance of obligate fruit-eating birds (Grass *et al.* 2013). Impacts can go beyond the immediate food source, for example, large eucalypt trees have been found to offer perching and nesting sites for raptor species, increasing their numbers (Ewbank 2000).

Eucalyptus camaldulensis was initially introduced into South Africa from Australia for forestry but has also become an important source of pollen and nectar for the apiculture industry

(Johannsmeier & Mostert 1995; Richardson *et al.* 2003). Although *Acacia mearnsii* is a more widespread invasive alien plant in the fynbos biome (Richardson & van Wilgen 2004), *E. camaldulensis* is an aggressive invader in most riparian areas (van Wilgen 2009). In a rapid assessment, Forsyth *et al.* (2004), notes that 46% of rivers in the Western Cape, which also contains the fynbos biome, were invaded by *E. camaldulensis*. There are no studies quantifying the extent and impacts of *E. camaldulensis* invasion in South Africa's riparian systems (Tererai *et al.* 2013), but eucalypts are known to decrease native plant diversity (Bernhard-Reversat 1999; Tererai *et al.* 2013) and reduce dragonfly diversity (Samways *et al.* 2011). However, very little is known about the impacts of invasive alien trees and *Eucalyptus* trees in particular, on bird assemblages in riparian areas.

Therefore, we assess how *E. camaldulensis* invasion affects riparian bird assemblages. Specifically we compare (1) bird species richness (2) bird abundance and (3) feeding guilds between invaded and near-pristine sites. Subsequently, we compare our results with studies from non-riparian tree invaded habitat.

2.2. Methods

2.2.1. Study area

The study was conducted along the Berg River, near the town of Hermon, north of Cape Town, South Africa (33° 26' 38.05"S; 18° 58' 24.70"E) (Fig. 2.1). The Berg River is a perennial 300 km long river with a catchment area of approximately 9000 km² (de Villiers 2007; Dzikiti *et al.* 2016). The study area is located Swartland shale renosterveld vegetation type of the fynbos biome (Mucina & Rutherford 2006). Climate is Mediterranean with a mean annual precipitation of 453 mm, with most rain received in June and the least in February (Mucina & Rutherford 2006). Mean daily temperatures range between 8-30°C (Mucina & Rutherford 2006).

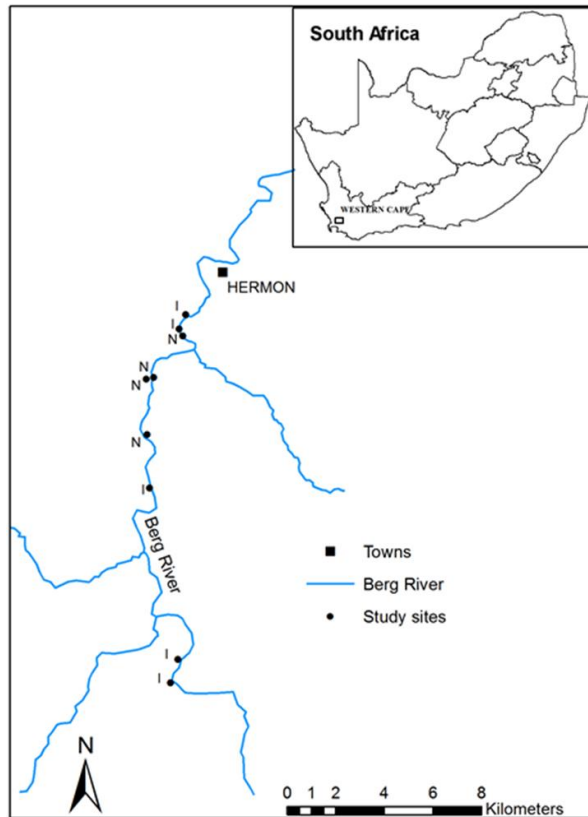


Figure 2.1. Locations of *Eucalyptus camaldulensis* invaded (I) and near-pristine (N) study sites along the Berg River in the Western Cape of South Africa.

Eucalyptus camaldulensis is the most abundant and prominent invasive alien tree species in the riparian area of the Berg River with other invasive alien tree species, mainly *Acacia mearnsii* and *Populus* species, being less abundant (also see Geldenhuys 2008). *Eucalyptus camaldulensis* invasion of the Berg River dates back about 50 years (Geldenhuys 2008). The remaining native vegetation occurs as small isolated remnants dominated by *Kiggelaria africana*, *Olea europaea* subsp. *africana*, *Podocarpus elongatus*, *Diospyros glabra* and *Searsia angustifolia* (Tererai et al. 2013).

2.2.2. Site selection

Two treatments were used for this study: near-pristine sites with few individuals of *Eucalyptus camaldulensis* and *Acacia mearnsii* (Fig. 2.2 a) and *E. camaldulensis* invaded riparian areas (Fig. 2.2 b) (Table S2.1). Near-pristine areas occur as small remnants of native vegetation; the only four remaining near-pristine areas were used in this study. Near-pristine sites are dominated by native vegetation with only a few individuals of *E. camaldulensis* occurring (less than 5% canopy cover; pers. obs.) since there were no sites entirely free of *E. camaldulensis* (Tererai et al. 2013). Due to the presence of other invasive tree species, invaded sites were

selected as to have *E. camaldulensis* cover exceeding 65%, mostly more than 90%, alien plants with the remainder consisting mainly of *A. mearnsii*.

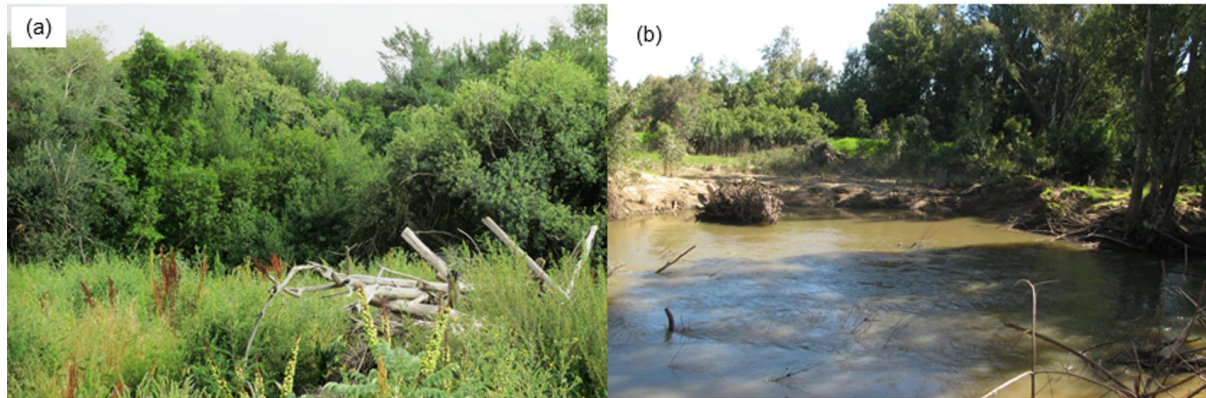


Figure 2.2. Near-pristine riparian vegetation (a) and (b) *Eucalyptus camaldulensis* invaded riparian vegetation.

2.2.3. Bird surveys

A total of 108 fixed-point bird counts (six per season for the nine sites) were done (Bibby *et al.* 2000). Half of these were done between 9 May and 5 September 2014 to represent winter and the other half between 15 September and 13 November to represent spring. Due to the small size of some near-pristine sites (Table S1) and to ensure independent samples, only one census point was sampled repeatedly for each site with a minimum of three days between sampling visits (Bibby *et al.* 2000). Vegetation in invaded sites could be dense; therefore a fixed maximum radius of 30 m was used. All birds within the 30 m fixed radius were identified audio-visually. Only birds that perched in the plot were recorded, except for the Brown-throated Martin and Yellow-billed Kite that rarely perch, and were therefore included when actively hunting for prey inside the plot.

Peak activity for most bird species occurs between dawn and midday, and sampling was therefore done from 30 minutes after dawn until 11h00 (Bibby *et al.* 2000). Sampling was conducted on days without mist, strong wind, high temperature or rain as these conditions affect bird activity and detection (Bibby *et al.* 2000). Counts were preceded by a two-minute resting phase to allow birds to settle and resume normal behaviour (Bibby *et al.* 2000). The total of 10 minutes allocated to bird counting was sufficient to observe all species, including cryptic and skulking species (pers. obs.). A voice recorder was used to record bird calls to confirm the visual field identification. Bird species were classified into eight feeding guilds according to their primary food sources (Table S2; Hockey *et al.* 2005). Birds of prey were placed in different

feeding classes, namely carnivores and raptors, to allow us to separately assess the impacts of *E. camaldulensis* on raptors.

2.2.4. Comparison of bird communities between riparian and non-riparian habitats

We compare the effect of alien tree invasion on bird assemblages in this study with that of non-riparian habitats (Greve *et al.* 2011; Rogers & Chown 2013; Thorpe 2013). These three studies were selected since they (1) are recent (2) used comparable methods and (3) were done in the same biome. To control for differences in time and area sampled, bird species richness and abundance data were divided by the sampling effort (time and area).

2.2.5. Data analyses

To assess if sampling had been adequate, sample-based rarefaction curves were calculated in PAST (Hammer *et al.* 2001). This method calculates the expected number of species when a given number of samples are drawn randomly, without replacement from a set of samples collectively representing an assemblage (Gotelli & Cowell 2001). With no significant difference in bird species richness and bird abundance between seasons (generalised linear model (GLM): $X^2 = 1.84$; $df = 1$; $P = 0.174$) data were pooled for all subsequent analyses.

Species richness (S), the Simpson diversity index ($1-D$) and the Simpson's evenness index ($E_{1/D}$) were used to compare bird assemblages between near-pristine ($n = 4$) and invaded ($n = 5$) sites. Diversity indices were calculated in PAST version 3 (Hammer *et al.* 2001). A Mann-Whitney U test (Statistica version 13; StatSoft Inc. 2016) was used to compare bird richness, bird abundance, Simpson's diversity and Simpson's evenness between near-pristine and invaded sites. The Simpson diversity index ($1-D$) increases with an increase in bird diversity (Magurran 2004). Simpson's evenness index ($E_{1/D}$) increases when bird abundance is equally distributed among species in the area and there are no dominant bird species (Magurran 2004).

Bird abundance, for individual species with more than ten sightings, was compared between invaded and near-pristine sites using a Mann-Whitney U test (Statistica version 13; StatSoft Inc. 2016). Additionally, we assessed whether bird body size is an important predictor of bird response to *E. camaldulensis* invasion (Polo & Carrascal 1999; Coetzee *et al.* 2013; Rogers & Chown 2013). Bird weight as a proxy for body size was compared between invaded and near-pristine areas with a Mann-Whitney U test (Statistica version 13; StatSoft Inc. 2016). All body weight measurements were obtained from Hockey *et al.* (2005). Differences in bird assemblages between sites were analysed with a principal component analysis (PCA) in SPSS version 22 (IBM Corp. 2013). A PCA graphically groups together sites with similar bird assemblages.

2.3. Results

2.3.1. Bird richness and abundance

Sampling was adequate; since the species accumulation curves had started to flatten off for both near-pristine and invaded sites (Fig S2.1). A total of 635 birds from 42 species ($n = 4$) in the near-pristine sites and 507 birds from 26 species ($n = 5$) in the invaded sites were sighted. There was a significant difference in bird species richness ($Z = -13.59$; $df = 1$; $P < 0.00$; Table 2.1) and bird abundance ($Z = -4.37$, $df = 1$, $P < 0.00$; Table 2.1) between invaded and near-pristine sites. Both Simpson's diversity index and Simpson's evenness were higher in near-pristine sites when compared to invaded sites (Table 2.1).

Table 2.1. Average bird species richness and abundance per sampling period for *Eucalyptus camaldulensis*-invaded and near-pristine sites along the Berg River, South Africa. A higher Simpson's diversity index ($1-D$) indicates the occurrence of more bird species at a higher abundance and a higher Simpson's evenness ($E_{1/D}$) indicates that bird species are equally abundant with no dominating bird species.

	Near-pristine	Invaded	Mann-Whitney U Test
Mean abundance \pm SD	158.8 \pm 6.5	101.4 \pm 8.3	$P < 0.00$
Mean richness \pm SD	18 \pm 4.2	12 \pm 1.8	$P < 0.00$
Simpson's diversity \pm SD	0.92 \pm 0.03	0.76 \pm 0.02	$P = 0.04$
Simpson's evenness \pm SD	0.51 \pm 0.03	0.34 \pm 0.03	$P = 0.02$

Eighteen species were lost from invaded sites whilst 24 species were shared between near-pristine and invaded sites (Fig. 2.3). Two species, the Red-eyed Dove and Forest Canary, occurred only in invaded sites.

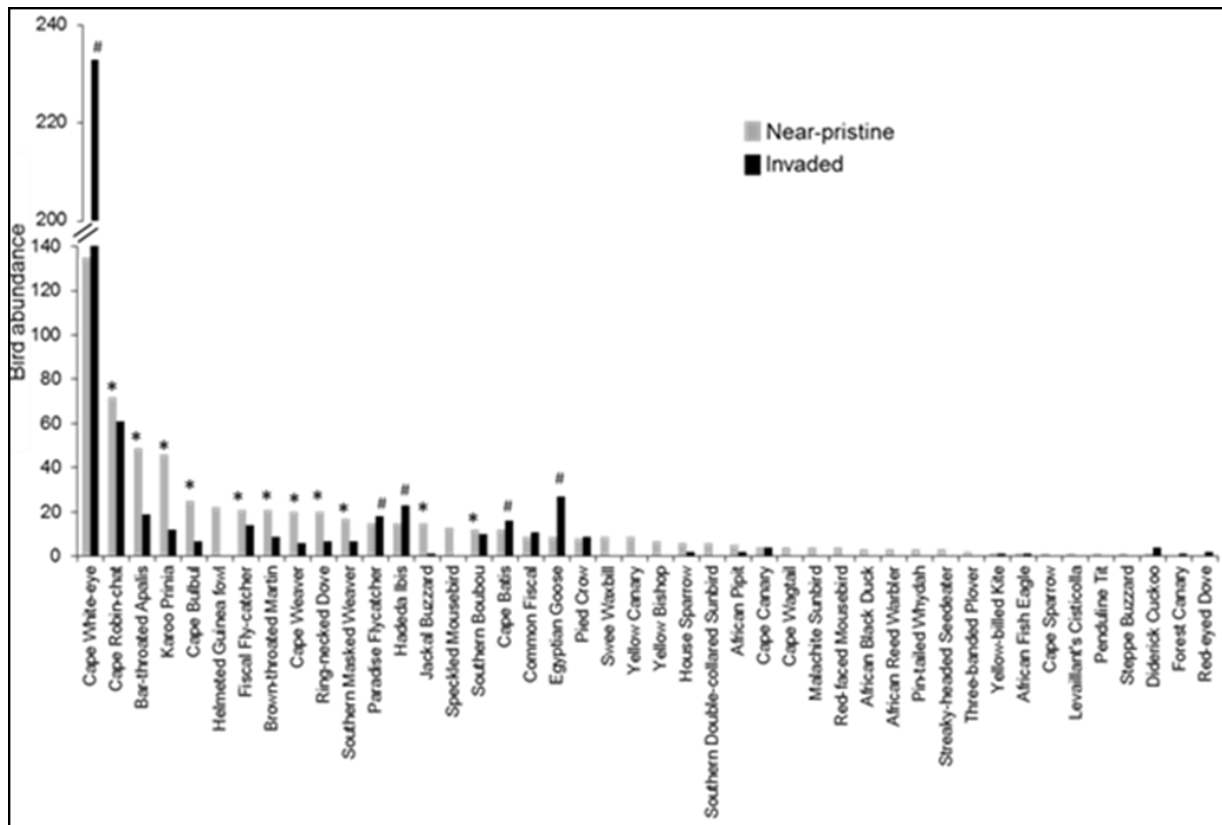


Figure 2.3. Comparison of individual bird species abundance between invaded and near-pristine sites. Bird abundance is the total number of individual birds recorded in invaded and near-pristine sites. The asterisk (*) indicates species with significantly higher abundances in near-pristine sites, while the hash (#) indicates species with significantly higher abundances in invaded sites. Only bird species with more than 10 sightings were included in the analyses.

There were more carnivorous bird species in invaded sites and herbivorous species occurred in equal numbers in invaded and near-pristine sites (Fig. 2.4). The total number of species for the remainder of the feeding guilds was lower for the invaded sites, with the nectar feeding guild absent from invaded sites (Fig. 2.4). Bird body weight did not differ between invaded and near-pristine sites ($Z = 0.53$; $df = 1$; $P = 0.6$).

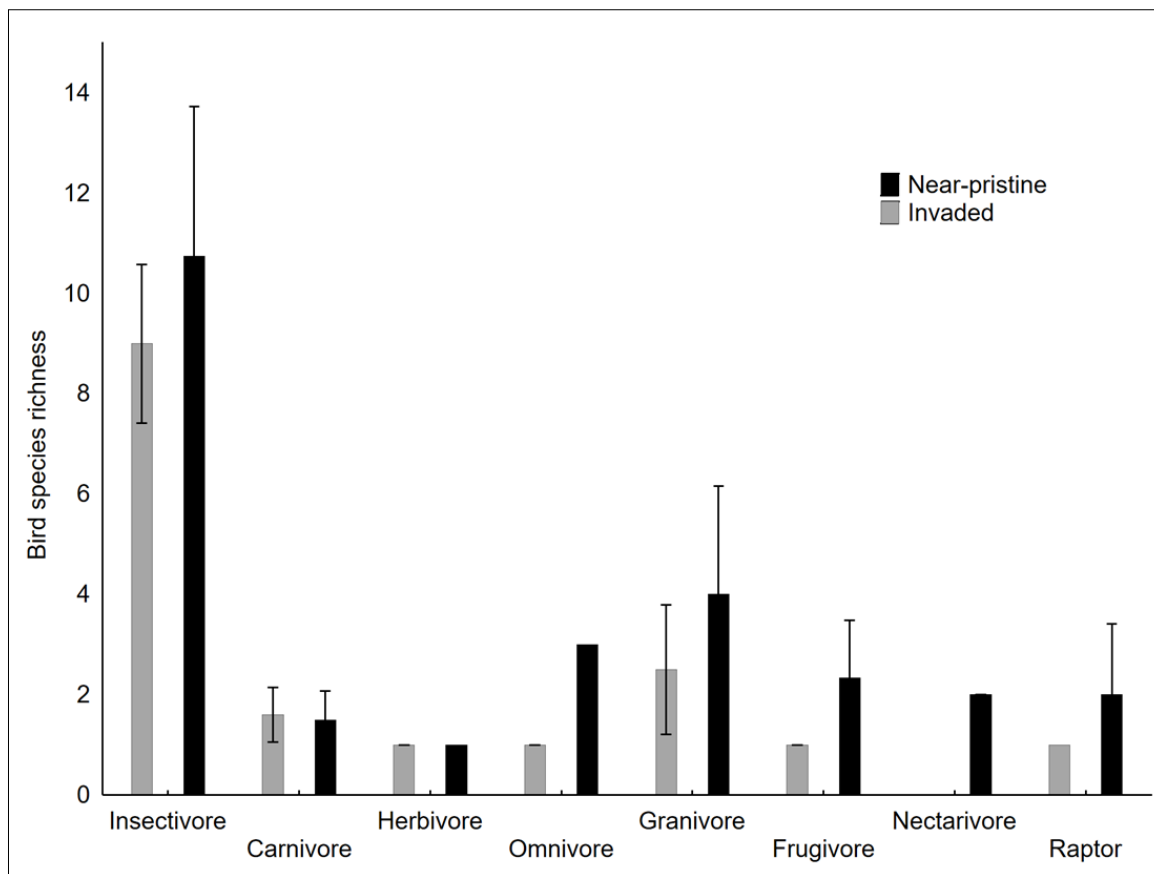


Figure 2.4. Bird species richness per feeding guild (total per site) for *Eucalyptus camaldulensis* invaded and near-pristine sites. Bars display the median and the data range is indicated by the whiskers.

A total of seven components were extracted with the PCA, with the first three components contributing the largest part (74 %) of the total variance (Table 2.2).

Table 2.2. Principal component analysis (PCA) showing components contributing most to the total variance in bird assemblages.

Component	Initial eigenvalues		
	Total	% Variance	Cumulative %
1	17.951	40.797	40.797
2	9.560	21.727	62.524
3	5.265	11.965	74.489

Bird species that make up the first principal components consist mainly of insectivores, granivores, nectarivores and frugivores (Table S2.3). Insectivores and granivores make up the

second principal component and the third component includes raptors, herbivores and granivores (Table S2.3). All invaded sites grouped together with one near-pristine site grouping closely to the invaded sites (Fig. 2.5). The other near-pristine sites distinctively separate from the invaded sites along all three principal components.

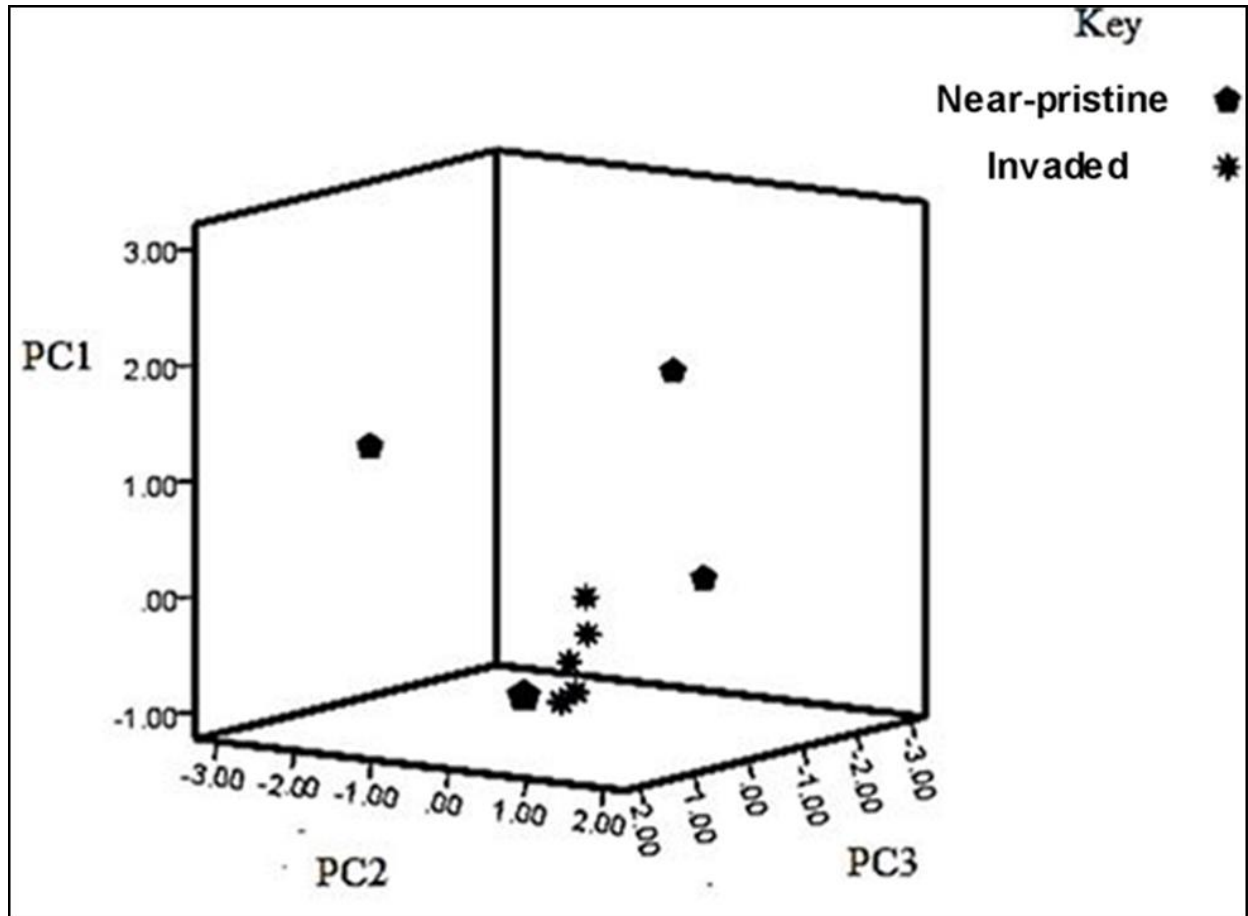


Figure 2.5. The grouping of *Eucalyptus camaldulensis* invaded and near-pristine sites along principal components 1, 2 and 3.

2.3.2. Comparison of bird communities between riparian and non-riparian habitats

Comparatively, riparian areas (whether invaded or near-pristine) have higher bird species richness and abundance than non-riparian habitats (Table 2.3). For both riparian and non-riparian habitats, bird species richness and abundance is highly variable but is lower in alien tree-invaded habitats. *E. camaldulensis* invasion had the highest impact on bird assemblages as more bird species are lost from invaded riparian areas compared to *Acacia* and *P. radiata*-invaded habitats (Table 2.3).

Table 2.3. Comparison of invasive tree impact on bird species richness and abundance in riparian and non-riparian fynbos areas. Bird species richness and abundance is presented as birds per hour (h)/hectare (ha). Values were calculated from paper appendices or from data provided by the authors.

Habitat type	Bird Species	Bird Species richness/h/ha	Bird abundance	Bird abundance/h/ha	Reference
<i>Pinus radiata</i> -invaded	26	1.1	819	34.9	Greve <i>et al.</i> (2011)
Mountain fynbos	33	1.4	1199	51.02	Greve <i>et al.</i> (2011)
<i>Acacia</i> -invaded: High density	33	0.09	2122	5.8	Rogers and Chown (2013)
Medium density	36	0.29	2154	17.6	Rogers and Chown (2013)
Low density	32	0.96	625	18.7	Rogers and Chown (2013)
<i>Acacia</i> -invaded	8	0.85	21	2.2	Thorpe (2013)
Strandveld	11	1.16	84	8.9	Thorpe (2013)
<i>Eucalyptus camaldulensis</i> -invaded	26	1.84	507	35.8	Current study
Fynbos riparian scrub	44	4.86	635	70.2	Current study

2.4. Discussion

2.4.1. Bird assemblages in invaded and near-pristine sites

Bird assemblages in *Eucalyptus camaldulensis*-invaded riparian habitats are largely a subset of those in near-pristine habitats. While invaded sites gained only two bird species (Red-eyed Dove and the Forest Canary), almost half of the 42 bird species present in near-pristine sites are absent in *Eucalyptus*-invaded sites. The Red-eyed Dove is known to be common in alien tree woodlands and especially in *Eucalyptus* stands (Hockey *et al.* 2005), but with only one individual of the Forest Canary sighted no inferences can be made for this species.

Of the 20 bird species occurring in both invaded and near-pristine sites, five species (Cape White-eye, Paradise Flycatcher, Hadedda Ibis, Cape Batis and the Egyptian Goose) had a significantly higher abundance in invaded sites (Fig. 2.3). Whilst the Cape Batis and Paradise

Flycatcher are forest dwellers, the Cape White-eye, Hadedda Ibis and the Egyptian Goose are opportunistic and are known to move into transformed habitats (Macdonald *et al.* 1986; Schwarzenberger & Dean 2003; van Rensburg *et al.* 2009; Dures and Cumming 2010). Invasive alien plants change the availability of resources, in particular food and nesting sites, which to a large extent determine the occurrence of birds (Holland-Clift *et al.* 2011). The Cape White-eye, Cape Batis and Paradise Flycatcher are foliage gleaners and their high abundance in invaded sites could indicate an increase in insect abundance (Fraser & Crowe, 1990) whilst the availability of nesting sites in the tall eucalypts trees could explain the higher abundance of the Hadedda Ibis and the Egyptian Goose (Fraser & Crowe 1990; pers. obs.).

The feeding guilds present in a bird community are largely determined by the availability of food resources (Symes *et al.* 2002). The results show that seven out of the eight feeding guilds still occur in the invaded sites but with frugivores, granivores, raptors and omnivores occurring at very low species richness when compared to near-pristine sites. Nectar feeding birds have completely disappeared from invaded sites. The low species richness of granivores and omnivores could be due to a decrease in the guilds' food resources in invaded sites. In their study, Tererai *et al.* (2013) note that invasion by *Eucalyptus camaldulensis* results in the replacement of fynbos riparian scrub vegetation by woodland with changes in understorey plant species composition. The decrease in the species richness of frugivores in *E. camaldulensis* invaded sites is in consistency with other studies where frugivores were also negatively affected by invasive alien plants (Fraser and Crowe 1990; Holland-Clift *et al.* 2011; Rogers and Chown 2013). As with other invasive alien woody plant species, *E. camaldulensis* invasion results in increased canopy cover with shading effects on understorey plants, affecting germination, growth and establishment of native plant species (Le Maitre *et al.* 2011; Tererai *et al.* 2013). An altered plant composition can lead to a change, decline or a lack of food resources for fruit-eating bird species (Hajzlerova and Reif, 2014).

Although only two specialist nectar feeding bird species (Fig. 4) occurred in near-pristine sites, and are lost from invaded sites, the nectar feeding guild is highly specialized and consists of very few species (Geerts & Pauw 2009). The two specialist nectar feeding bird species found in near-pristine sites is not unusually low, but both species are lost in invaded sites (Fig. 5). Consequently nectar feeding bird abundance also changes from 4 birds in near-pristine to no birds in invaded areas (Table 2). Specialist nectar feeding birds are strongly linked to their specialist food resources and the absence of bird pollinated plants in *Eucalyptus* invaded sites can explain the absence of this guild (Grey *et al.* 2007; Geerts & Pauw 2009; Geerts *et al.*

2011). Similarly, other studies have found invasive alien plants to displace specialist nectar feeding birds (Fraser & Crowe 1990; Greve *et al.* 2011; Rogers & Chown 2013; Thorpe 2013). However, the opposite is true when the invasive alien plant species provides an abundant nectar source (Le Roux *et al.* 2010; Geerts *et al.* 2013). *Eucalyptus camaldulensis* invasions change the understorey plant species composition, which contains nectar rich plants, but not the percentage canopy cover (chapter 3 of this thesis). Bird species dependent on structure will tolerate invasive trees, whilst the altered plant composition, such as the loss of nectar plants, will lead to a decline or absence of certain feeding guilds (Hajzlerova & Reif 2014).

The importance of eucalypts to raptor species is not apparent from this study as the richness and abundance of raptors is slightly lower at invaded sites. This dilutes the argument that eucalypts are important to raptor species for roosting, nesting and to serve as hunting platforms (Ewbank 2000; Suddjian 2004; Cilliers & Siebert 2012; Carnie 2015). The importance of *Eucalyptus* trees as a hunting platform might be explained when an occasional tall *Eucalyptus* tree occurs within indigenous vegetation or in an urban environment where large trees are scarce, but here we show that this effect disappears in a *Eucalyptus* dominated landscape. Dean *et al.* (2002) also notes that there is a decrease in prey species in monospecific alien tree stands and this may explain the low raptor species richness and abundance in the invaded sites. Alternatively, the small scale at which the study was conducted can potentially explain this decrease, since raptors require large home ranges (Lindenmeyer *et al.* 2002). However, with only 14 sightings of four raptor species, this requires more study.

The potential importance of a few tall trees within native vegetation to raptors is highlighted in the principal component analysis. Three near-pristine sites group together along all three principal components suggesting a similarity of the site characteristics as shown by the birds making up the principal components. However, the raptors occur along the third principal component which is the near-pristine site with the tallest trees (*Podocarpus elongatus*). This site consequently also groups closely with the invaded sites. Another potential reason for the close grouping of this site with invaded sites, and unexpectedly so, is that the understorey plant component is largely absent, which is typical of *E. camaldulensis* invaded areas.

2.4.2. Comparison of bird communities between riparian and non-riparian habitats

Bird species richness in invaded vegetation from all four studies; that is in *E. camaldulensis*, *P. radiata* or *Acacia* stands is lower when compared to near-pristine sites. We acknowledge that even though we corrected for sampling intensity (time and space), longer observation periods will always result in fewer species per time unit. Despite this, a strong pattern provides

confidence in the riparian versus non-riparian comparison with impacts on bird assemblages being higher in *Eucalyptus* invaded areas, than in *Acacia* and *Pinus* invaded areas. Lower effects from invasion by *Acacia* and *P. radiata* might be attributed to the type of ecosystem affected (Sogge *et al.* 2008). It is also possible that the lower effect from invasion could be due to a larger regional pool of bird species available that can adapt and tolerate habitat change through invasion (Brown *et al.* 2001) or the part of the invasion cycle the system is in. Thus bird species from surrounding areas migrate into the invaded habitats, compensating for losses from invasion (Brown *et al.* 2001; Rogers & Chown 2013).

2.4.3. Conclusion

Riparian habitats act as important refugia for wildlife in highly transformed landscapes, but here we show support for the hypothesis that the invasion by alien trees has negative impacts on bird assemblages. Significantly though is that we show that some of the most critical avi-faunal ecosystem services are impacted the most, namely seed dispersal and pollination. Consequently, and in conjunction with studies on plant communities and water runoff, our results strongly support the removal of *E. camaldulensis* from riparian areas. However, whether the tree removal and passive restoration activities can restore riparian bird assemblages to pre-infestation levels needs to be determined.

2.5. Acknowledgements

We acknowledge funding from the DST-NRF Centre of Excellence for Invasion Biology and the Working for Water Programme through their collaborative research project on “Integrated Management of invasive alien species in South Africa”. Funding to SG was also provided by the National Research Foundation (Grant 87843). We thank the landowners who allowed access to their properties and Michelle Slabber for fieldwork assistance. We thank Joseph Kioko and Mirijam Gaertner for comments on an earlier draft.

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Supplementary tables

Table S2.1. Invasion condition, coordinates, site sizes (ha), site maximum plant height (ha) and site canopy cover (%) for the study sites.

Invasion condition	Coordinates	Size (ha)	Maximum plant height (m)	Canopy cover (%)
Invaded	-33.58638; 18.91365	2.4	9	94.2
Invaded	-33.56855; 18.93551	11.8	12	85.5
Invaded	-33.44900; 18.95300	4.6	12	57.4
Invaded	-33.58700; 18.94600	12.5	9	89.8
Invaded	-33.44941; 18.95109	3.7	12	77.7
Near-pristine	-33.47300; 18.93900	5.6	3.6	87.6
Near-pristine	-33.45800; 18.95000	3.8	5	42
Near-pristine	-33.44700; 18.95607	1.6	5.5	100
Near-pristine	-33.47500; 18.93800	5.1	6	100

Table S2.2. Common names, scientific names and feeding guilds for all bird species observed in this study.

Common name*	Scientific name*	Feeding guild*	Food source	Bird Weight*
Bar-throated Apalis	<i>Apalis thoracica</i>	Insectivore	Insects, spiders, seeds and fruit	9- 13g
Cape Batis	<i>Batis capensis</i>	Insectivore	Small insects	10-14g
Yellow Bishop	<i>Euplectes afer</i>	Granivore	Seeds and insects	25-50g
Southern Boubou	<i>Laniarius ferrugineus</i>	Insectivore	Invertebrates, reptiles, mice, fruit	45-68g
Cape Bulbul	<i>Pycnonotus capensis</i>	Frugivore	Fruits, seeds, nectar, insects	30-46g
Jackal Buzzard	<i>Buteo rufofuscus</i>	Raptor	Small mammals, reptiles, birds, frogs, insects	900-1700g
Steppe Buzzard	<i>Buteo vulpinus</i>	Raptor	Small mammals, reptiles, birds and frogs	510-700g
Cape Canary	<i>Serinus canicollis</i>	Granivore	Seeds, fruit, flower, insects	12-22g
Forest Canary	<i>Crithagra scotops</i>	Granivore	Seeds, fruit, flowers, leaves, insects	12- 20g
Yellow Canary	<i>Crithagra flaviventris</i>	Granivore	Seeds and small fruit	17-18g
Cape-Robin Chat	<i>Cossypha caffra</i>	Insectivore	Invertebrates, fruits	23-38g
Leviallant's Cisticolla	<i>Cisticola tinniens</i>	Insectivore	Insects	410-610g
Pied Crow	<i>Corvus albus</i>	Omnivore	Fruit, seeds, insects, frogs	35g

Diderick's Cuckoo	<i>Chrysococcyx vaprius</i>	Insectivore	Insects, other invertebrates	190-300g
Red-eyed Dove	<i>Streptopelia semitorquata</i>	Granivore	Seeds, bulbs, insects	100-160g
Ring-necked Dove	<i>Streptopelia capicola</i>	Granivore	Seeds, nectar, invertebrates	780-1280g
African black Duck	<i>Anas sparsa</i>	Omnivore	Plants, invertebrates	2000-3800g
African Fish Eagle	<i>Haliaeetus vocifer</i>	Raptor	Fish, birds, reptiles, carrion	26g
Fiscal Flycatcher	<i>Sigelus silens</i>	Insectivore	Insects, grasshoppers, moths	11-17g
Paradise Flycatcher	<i>Terpsiphone viridis</i>	Insectivore	Insects	25-50g
Common Fiscal	<i>Lanius collaris</i>	Carnivore	Invertebrates, reptiles, birds	800-1500g
Helmeted Guinea Fowl	<i>Numida meleagris</i>	Omnivore	Bulbs, leaves, seeds, insects	1500-3500g
Egyptian Goose	<i>Alopochen aegyptiaca</i>	Herbivore	Grass, seeds	1000-1100g
Hadedda Ibis	<i>Bostrychia hagedash</i>	Carnivore	Invertebrates , worms	570-700g
Yellow-billed Kite	<i>Milvus aegyptius</i>	Raptor	Small mammals, reptiles, frogs, insects, small birds	10-16g
Brown-throated Martin	<i>Riparia paludicola</i>	Insectivore	Insects	40-70g
Red-faced Mousebird	<i>Urocolius indicus</i>	Frugivore	Fruits, flowers, leaves, nectar	35-65g
Speckled Mousebird	<i>Colius striatus</i>	Frugivore	Fruits, buds, leaves, nectar	22-28g

African Pipit	<i>Anthus cinnamomeus</i>	Insectivore	Insects	8-11g
Karoo Prinia	<i>Prinia maculosa</i>	Insectivore	Insects and spiders	28-45g
Streaky-headed Seedeater	<i>Crithagra gularis</i>	Granivore	Seed, fruit flowers, buds, nectar, insects	22-36g
Cape Sparrow	<i>Passer melanurus</i>	Granivore	Seed, fruit flowers, buds, nectar, insects	22-30g
House Sparrow	<i>Passer domesticus</i>	Granivore	Seeds, fruit, buds, nectar, insects	11-25g
Malachite Sunbird	<i>Nectarinia famosa</i>	Nectarivore	Nectar, insects, spiders	6-10g
Southern double Collared Sunbird	<i>Cinnyris afer</i>	Nectarivore	Nectar, insects, spiders	7.5g
Cape Pendulline- Tit	<i>Anthoscopus minutus</i>	Insectivore	Insects, larvae, spiders beetles	18-24g
Cape Wagtail	<i>Motacilla capensis</i>	Insectivore	Insects, small fish, reptiles, tadpoles	8-14g
African Reed Warbler	<i>Acrocephalus baeticatus</i>	Insectivore	Insects	54g
Cape Weaver	<i>Ploceus capensis</i>	Insectivore	Insects, fruits, buds	30-44g
Southern Masked Weaver	<i>Ploceus velatus</i>	Insectivore	Insects, fruit, nectar, seeds	8-12g
Cape White-Eye	<i>Zosterops virens</i>	Insectivore	Insects, fruit, nectar	8-12g
Pin-tailed Whydah	<i>Vidua macroura</i>	Granivore	Seeds, insects	13-17g

*Feeding guild classification, bird names and bird weight measurements based on Hockey *et al.* (2005). Birds were categorised based on the following main food sources (main food component makes up to > 50% of food consumed): Carnivore- Large arthropods and vertebrates; Frugivore- Fleshy fruits; Granivore- Seeds; Herbivore- Plant material; insectivore- Insects; Nectarivore- Nectar; Raptor- Vertebrates, birds and small mammals; Omnivore- 2 or more of the above.

Table S2.3. Component matrix showing the bird species making up the first 3 components in the PCA. The values highlighted in bold are the contributions of each species to the principal components and birds are listed in the order of importance on the principal components axis.

Bird species	Principal component		
	1	2	3
Speckled Mousebird	.959	.146	.210
Red-faced Mousebird	.936	-.205	.238
Southern Double Collared Sunbird	.936	-.205	.238
African Reed Warbler	.936	-.205	.238
Cape Bulbul	.868	.200	.405
Brown-throated Martin	.825	.439	-.137
African Pipit	.835	-.476	.114
Levaillant's Cisticolla	.795	.580	.131
African Black Duck	.795	.580	.131
Penduline Tit	.795	.580	.131
Cape Wagtail	.795	.580	.131
Three-banded Plover	.795	.580	.131
Pin-tailed Whydah	.795	.580	.131
Karoo Prinia	.761	-.422	-.100
Cape Robin Chat	.709	-.131	-.357
Swee Waxbill	.691	.565	-.349
Southern Boubou	.686	.612	-.247
Bar-throated Apalis	.675	.091	.027
Egyptian Goose	-.568	.338	.671
Yellow Bishop	-.411	.196	.592
Cape Batis	-.362	.502	.382
Steppe Buzzard	-.246	.138	.532

Cape Canary	.265	.519	-.372
African Fish Eagle	-.085	.268	.518
Jackal Buzzard	-.077	.352	-.140

Supplementary figure

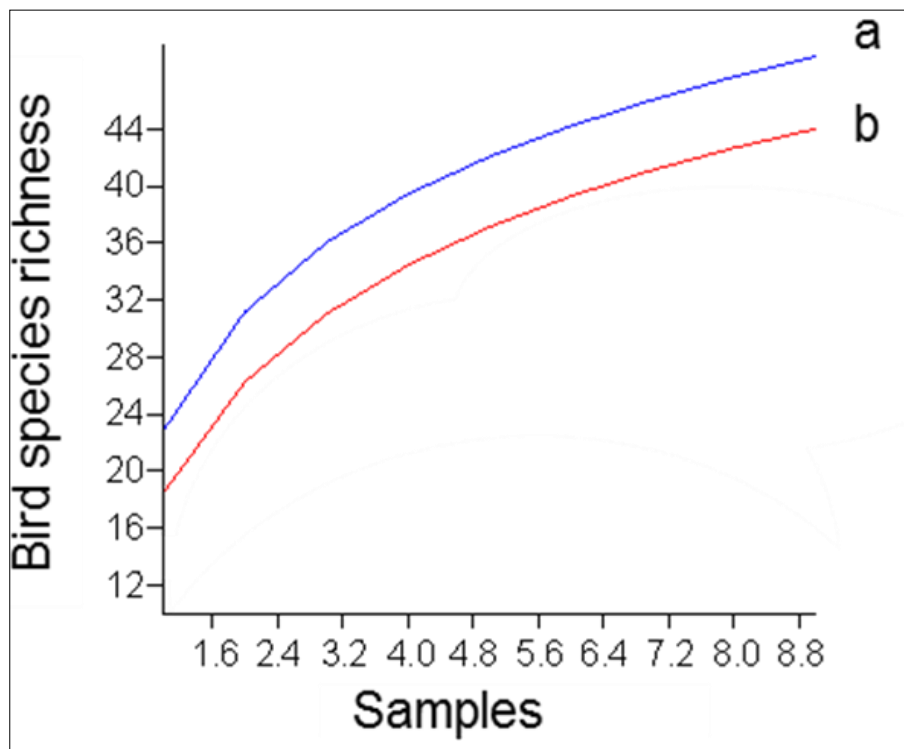


Figure S2.1 Mao Tau sample-based rarefaction curves showing species richness estimates for a) near-pristine and b) invaded sites.

CHAPTER THREE

RECOVERY OF BIRD AND PLANT ASSEMBLAGES FOLLOWING REMOVAL OF AN ALIEN TREE INVADER FROM THE RIPARIAN HABITAT OF THE BERG RIVER, SOUTH AFRICA

Abstract

Invasion by alien trees is common in riparian ecosystems across the world. Restoration of affected areas largely focuses on removing the invader, leaving the ecosystems to “self-repair” without additional initiatives such as planting native species. Consequently, there is a need to evaluate passive ecosystem recovery after invasive tree clearing. We assess native vegetation and bird assemblages as indicators of ecosystem processes’ recovery. As a case study, we use the riparian ecosystem of the Berg River, which is one of the most invaded systems in the Cape Floristic Region of South Africa. Here, clearing of alien trees, mainly *Eucalyptus camaldulensis*, has been on-going for over a decade. We employ a chronosequence (space for time substitution) approach, comparing plant and bird assemblages between invaded sites, near-pristine sites and sites cleared in 2005, 2007, 2008 and 2014. A total of 2049 birds from 53 species was recorded, with significantly lower bird species richness and bird abundance in invaded sites compared to cleared and near-pristine sites. However, cleared and near-pristine sites had similar bird species richness and abundance. While there is a steady increase in bird assemblages with time since clearing, bird species richness and abundance do not fully recover. We recorded fifty five plant species (27 native, 28 alien) from 50 genera and 31 families across invasion conditions. Significantly higher plant species richness occurred in cleared sites with invaded sites having the lowest species richness. Native plant species richness increased post-clearing, but so did alien forbs and graminoids. Indigenous tree species were rare or absent. Invasion condition, canopy cover and surrounding land-use were important predictors of bird richness and bird abundance. Populations of birds in all feeding guilds, except raptors, gradually increased after clearing. To aid the process of restoration, we suggest active re-introduction of key riparian shrub and tree species such as *Podocarpus elongatus*, *Brabejum stellatifolium*, *Cunonia capensis* and *Salix mucronata* subsp. *hirsuta* together with shrubs such as *Euclea tomentosa* and *Leonotis leonorus* which are easy to propagate, improve vegetation structure, increase food resources and should subsequently aid the complete recovery of riparian bird assemblages.

Key words: Alien plant clearing, Biological indicators, Natural vegetation recovery, Post-clearing monitoring.

3.1. Introduction

Riparian habitats provide channels for the transportation of propagules and matter from catchment areas to low altitude areas (Naiman & Decamps 1997). Additionally, disturbances through natural processes and degradation by human activities make riparian zones highly susceptible to alien plant invasions (Planty-Tabacchi *et al.* 1996; Naiman and Decamps 1997; Esler *et al.* 2008). Invasion of riparian areas by alien plants have several impacts, with the most important impacts being reduction in water runoff, lower biodiversity and disruption of ecosystem services (Hood & Naiman 2000; Richardson *et al.* 2007; Holmes *et al.* 2008). Since most habitats have been affected, invasive alien plants have become a global challenge for conservation managers and are listed as the second largest threat to conservation, after direct habitat loss (Wilcove *et al.* 1998; Wilcove & Chen 1998)

Invasive alien plants often cover large areas of land and restoring these areas is a complicated and expensive process (Zavaleta *et al.* 2001; Gaertner *et al.* 2012). Due to financial limitations, most restoration projects use the passive option whereas removal of the degrading factor, such as invading plants leaves the ecosystem to recover naturally from soil-stored seed banks and seeds dispersed from remnant native vegetation (Roberts & Gilliam 2003; Impson *et al.* 2013). Where successful recovery of ecosystem processes and services is not realised, active restoration, which involves additional actions other than removing the invader, are sometimes employed (Esler *et al.* 2008). Thus, passive restoration is cost-effective since it is based on the assumption that ecosystem recovery occurs unassisted. However, this assumption is rarely quantified as habitat monitoring following passive restoration is rarely done, and where it is carried out, the focus is on vegetation recovery with little attention on the recovery of other taxa (Golet *et al.* 2008).

Monitoring and evaluation is important to assess passive restoration success and to establish if there is need for further interventions (Kentula 2000; Zavaleta *et al.* 2001; Heleno *et al.* 2010). Regardless of the need for well-rounded assessments following restoration, most studies have a botanical focus (e.g. Galatowitsch & Richardson 2005; Blanchard & Holmes 2008; Ruwanza *et al.* 2013a; Kerr & Ruwanza 2016; Ndou & Ruwanza 2016). However, despite being still limited, post-clearing evaluation studies have recently started to focus more on animal communities (e.g. Shanahan *et al.* 2011; Magoba & Samways 2010; Heleno *et al.* 2010; Samways *et al.* 2011; Atkinson *et al.* 2015; Maoela *et al.* 2016a, b). Assessments of animal communities after invasive alien plant clearing remain rare due to the assumption that recovery of native plants enhances animal communities' recovery and consequently, ecosystem processes and services (Atkinson *et al.* 2015). Thus, the response of animal communities to alien plant clearing is less well

understood (but see for e.g. Magoba & Samways 2010; Samways *et al.* 2011). Bird assemblages are particularly useful as indicators to assess ecosystem recovery following invasive alien plant clearing since birds are mobile, reliably identified, feed at different trophic levels and respond quickly to changes in plant diversity and vegetation structure (Dobson *et al.* 1997; Burnett *et al.* 2005; Majer 2009). For these reasons, the recovery of bird assemblages can serve as a reflection of the responses of other faunal communities (Fox & Hockey 2007).

In South Africa, riparian areas are the most severely invaded systems and are mainly invaded by *Acacia*, *Hakea*, *Eucalyptus* and *Prosopis* species (Le Maitre 2000; Mondlane *et al.* 2001; Forsyth *et al.* 2004; Richardson & van Wilgen 2004). The greatest impact of these tree species' invasions is a further decrease of the country's already limited water supplies (Le Maitre *et al.* 2000; Le Maitre *et al.* 2002; Forsyth *et al.* 2004; Dzikiti *et al.* 2016). Consequently, the Working for Water (WfW) programme was established in 1995 as a government sponsored initiative through the Department of Environmental Affairs to control alien plant invasions (van Wilgen *et al.* 1998; Esler *et al.* 2008). Although they also clear alien plants from terrestrial systems and contribute towards biodiversity conservation, the main aim of the WfW is to clear alien plants from riparian areas to mitigate against the loss of scarce water resources (van Wilgen *et al.* 1998; Esler *et al.* 2008). They employ a passive restoration approach and consider the removal of the invasive alien plants as a final goal (Galatowitsch & Richardson 2005), but this mechanism of restoration does not always lead to ecosystem recovery. Although there are studies showing that autogenic recovery may take place in areas where restoration thresholds have not been crossed, a failure of indigenous vegetation to recover often result in secondary invasions (Hobbs & Harris 2001; Galatowitsch & Richardson 2005; Blanchard & Holmes 2008; Ruwanda *et al.* 2013). In such cases, invasive alien plant clearing cannot be considered as an ultimate action but first step in ecosystem restoration (Holmes & Cowling 1997).

Here we investigate changes in bird assemblages in response to *Eucalyptus camaldulensis* clearing from a riparian habitat. We employ a chronosequence (space for time substitution) method to evaluate plant and bird assemblages at cleared sites and compare these with a reference community. The technique is useful to assess passive restoration success and guiding active restoration efforts (Palmer *et al.* 2007). We determine if plant and bird assemblages in cleared sites recover to near-pristine levels and use bird assemblages as an indicator to guide active restoration. We hypothesize (i) that the plant communities in recently cleared sites will not have returned to near-pristine diversity and structure, (ii) that recently cleared sites will have depauperate bird assemblages, due to low plant diversity and absence of vegetation structure and (iii) that the oldest cleared sites will have regained plant diversity and vegetation structure,

hence supporting similar bird communities as near-pristine sites. Alternatively, plant communities' recovery does not correlate with bird assemblage recovery, and bird assemblages are determined by other variables.

3.2. Methods

3.2.1. Study area

The study was done along the Berg River, between the towns of Wellington and Hermon, South Africa (33° 26' 38.05"S; 18° 58' 24.70"E) (Fig. 3.1). The Berg River is perennial, flowing approximately 300 km from source to mouth with a catchment area of approximately 9000 km² (de Villiers 2007; Dzikiti et al. 2016). The area falls within the Swartland shale renosterveld vegetation type (Mucina & Rutherford 2006). Climate is Mediterranean with average daily temperatures ranging from 8-30°C (Mucina & Rutherford 2006). Mean annual precipitation is 453 mm, with June being the wettest and February the driest month (Mucina & Rutherford 2006).

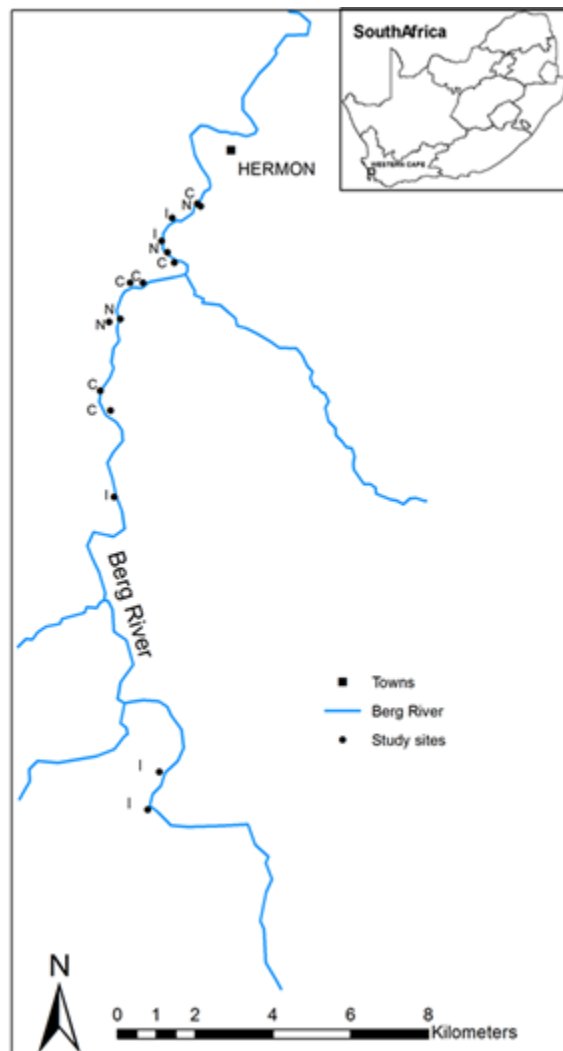


Figure 3.1. Locations of invaded (I), cleared (C) and near-pristine (N) sites along the Berg River in the Western Cape of South Africa.

The invasive alien *Eucalyptus camaldulensis* is the most dominant tree in the Berg River catchment, with small pockets of native vegetation remaining (Geldenhuys 2008). Native vegetation largely constitute of *Kiggelaria africana*, *Olea europaea* subsp. *africana*, *Podocarpus elongatus*, *Diospyros glabra* and *Searsia angustifolia* (Tererai *et al.* 2013).

We used three treatment types made up of six sites cleared in 2005 (two sites), 2007 (two sites), 2008 (one site) and 2014 (one site) plus five invaded and four near-pristine sites as a reference. Clearing entailed WfW cutting down trees, and later removing biomass with no burning applied to the sites. Sizes of the cleared sites range from 4.6 ha to 15.3 ha (Table S3.1). The only four remaining near-pristine sites were used as reference sites and sizes ranged from 1.6 ha to 5.6 ha. Two of the near-pristine sites are dominated by native vegetation with only a few individuals

of *Eucalyptus camaldulensis* occurring since there were no other sites totally free from this species (Tererai *et al.* 2013). Invaded sites are described as those in which *E. camaldulensis* cover exceeds 65%. Site sizes of invaded sites range between 2.4 ha and 12.5 ha.

3.2.2. Vegetation surveys

The following plant characteristics important for birds were surveyed: plant diversity (plant species richness and abundance), plant structure (plant height and canopy cover), plant composition (plant growth forms) and whether plants had fruits, flowers or seeds at the time of sampling. A total of two plant surveys were conducted per site (n = 15) for winter and spring resulting in a total of 30 surveys. Surveys were done using line transects extending from the centre of each bird count station for 30 m (James & Shugart 1970). Vegetation on the river bank and adjoining floodplain were included but aquatic submerged and emergent plants were excluded.

The point intercept method was used, dropping a vegetation height pole with 10 cm vertical demarcations every 2 m along transects. All plants that came into contact with the vegetation pole were identified and plant species richness was determined. Species' specific cover was calculated to measure the abundance of individual species. At several points along transects, multiple hits of plants were common and total abundance for some transects exceeded 100%. Canopy cover was visually determined every 2 m along transects and scored as present or absent to calculate total percentage canopy cover per transect. Plant height was determined at all points and the number of plants along transects which had flowers, fruits or seeds at the time of sampling were recorded.

To determine plant composition, plants were classified as indigenous or alien according to Goldblatt and Manning (2000) and Bromilow (2010). Species were assigned to broad growth forms: trees, shrubs, forbs, geophytes (perennial plants that are propagated by buds on underground bulbs, tubers or corms), graminoids (grasses, sedges and restioids -reed-like plants that belong to the *Restionaceae* or Cape Reed family) and vines (creeping and climbing plants) (Goldblatt & Manning 2000).

3.2.3. Bird surveys

The fixed-point count method was used to conduct bird surveys (Bibby *et al.* 2000). All birds seen and/or heard within 30 m were recorded. Fixed-point counts are essentially transects of which the observer performs the count in a 360° arc around a fixed survey station (Bibby *et al.* 2000). Bird surveys were done on days with no rain, mist, high temperatures or strong winds as

these weather conditions affect bird activity and detection (Bibby *et al.* 2000). Surveys commenced at approximately 30 minutes after dawn and continued to mid-morning as bird activity declines after this time. Birds were given a two-minute resting phase allowing them to resume activities following arrival of the observer at a survey station after which counts were conducted for a total of 10 minutes (Bibby *et al.* 2000). Only birds that actively utilised or perched within a 30 m radius were recorded. Brown-throated Martins and Yellow-billed Kites are bird species that rarely perch and were only recorded when they were actively hunting for prey. Bird species were classified into eight feeding guilds namely; insectivores, nectarivores, frugivores, carnivores, raptors, herbivores, granivores and omnivores (Table S3.2) (Hockey *et al.* 2005). Birds of prey were placed in different feeding classes namely, carnivores and raptors due to a need to assess if indeed invasive alien plants benefit raptor species.

Bird sampling was carried out in cleared sites and the same bird data used for invaded and near-pristine sites (see Chapter 2) was used in this chapter. Only one census point was used for each cleared site thus substituting space for time by repeatedly sampling the same sites (Bibby *et al.* 2000). A site was sampled more than 3 days apart, constituting independent data points. Six surveys were conducted per cleared site ($n = 6$) during winter (19 May to 9 September 2014) and spring (15 September to 13 November). In total, 72 bird surveys were carried out for cleared sites during the study.

3.2.4. Data analyses

Plant variable analyses were done using one-way ANOVA (Statistica version 13; StatSoft Inc. 2016) after checking for normality using Shapiro–Wilk test. We evaluated differences in native and alien plant species richness and plant species composition (using plant growth forms) between invaded, near-pristine and cleared sites. The Tukey’s HSD test was used to determine differences among the three treatments.

Data on bird assemblages and habitat characteristics was not normally distributed after transformation. A generalised linear model (GLM) with Poisson distribution and a log-linked function was used to test the effects of habitat characteristics on bird assemblages. All analyses were done in R (R Development Core Team 2012). Both categorical and continuous predictors were used. We considered the following predictor variables on bird species richness and bird abundance: invasion status (invaded, cleared, uninvaded), maximum plant height and percentage canopy cover, plant species richness, total plants with flowers, total plants with fleshy fruits and total plants with seeds, season (winter and spring) and surrounding land-use (wheat farming, vineyards and pomegranate orchards). Surrounding land-use was included

since all study sites are located in a mosaic of agricultural land with potentially different impacts on bird assemblages.

3.3. Results

3.3.1. Response of plant assemblages to invasion and removal of *Eucalyptus camaldulensis*

A total of 55 plant species (27 native and 28 alien) from 50 genera and 31 families were recorded. Spring had significantly more plant species than winter ($F = 4.28$, $df = 1$, $P < 0.01$); similar trends were found in near-pristine, invaded and cleared sites. There was a significant difference in species richness across invasion condition ($F = 313$, $df = 2$, $P = 0.00$) with more species occurring in cleared sites (Fig. 3.2 a). A further comparison of the cleared sites showed that there is a significant difference in species richness ($F = 1867.7$, $df = 5$, $P = 0.00$) with earliest cleared sites having more native plant species (Fig. 3.2 b).

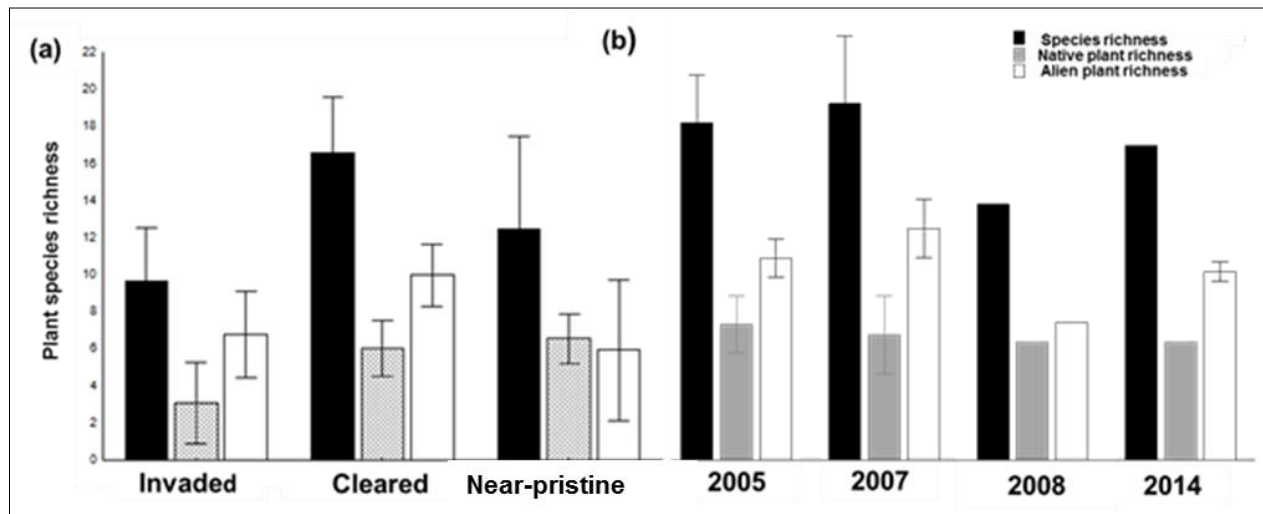


Figure 3.2. Comparison of (a) plant species richness: total, native and alien; (b) plant species richness: total, native and alien over time since clearing. Bars show means \pm SD.

Near-pristine sites had 27 (14 native), invaded had 31 (11 native) and cleared had 37 (16 native) plant species (Fig. 3.2 a). Invasion by *Eucalyptus camaldulensis* resulted in the displacement of 12 plant species, nine of them native trees and shrubs including overstorey species such as *Podocarpus elongatus*, *Olea europea* subsp. *africana* and *Rhus angustifolia*. Native plants species increased in richness post-clearing with significantly more natives in cleared and near-pristine sites ($F = 1020.8$, $df = 2$, $P < 0.001$).

Significantly more alien plants occurred in cleared sites compared to near-pristine sites ($F = 177.14$, $df = 2$, $P < 0.01$) with ten of these alien species being herbaceous plants. There was a steady increase in native plant richness with time since clearing although not significantly so

(Fig. 3.2 b). After clearing, there was a drop in the percentage contribution of trees whilst the percentage contribution of forbs, graminoids and shrubs increased (Fig. 3.3 a). Only two native tree species (*Olea europaea* subsp. *africana* and *Kiggelaria africana*) were recorded in cleared sites. There are no apparent trends in the percentage contribution of growth forms with time since clearing.

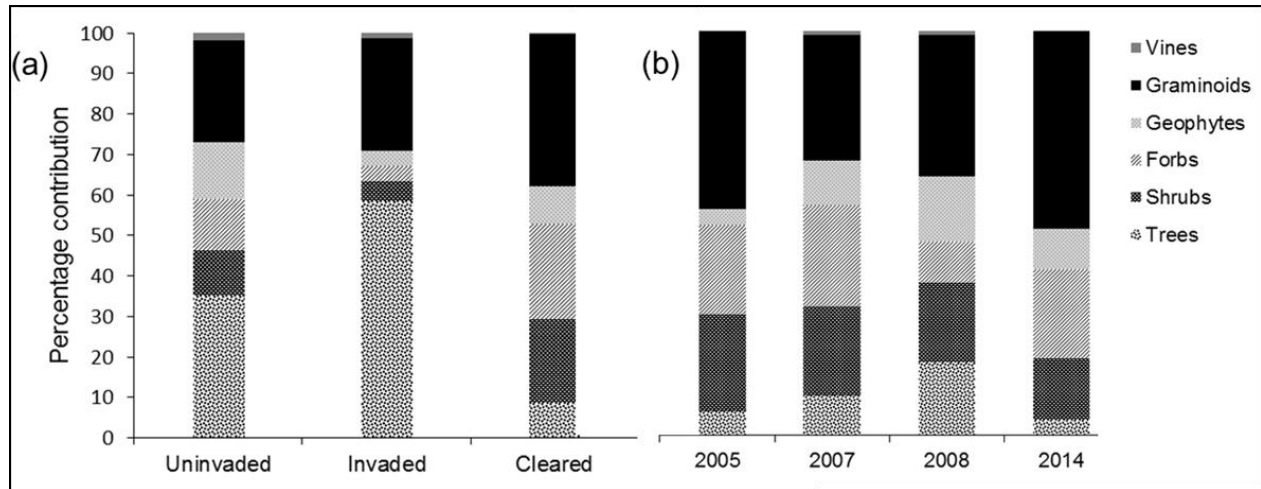


Figure 3.3. Percentage contribution of different growth forms (alien and native plants) in (a) near-pristine, invaded and cleared sites (average of all cleared sites) and in (b) sites cleared in different years, all sampled in 2014.

Sixteen new species, not recorded in invaded or reference sites five of them alien herbs and graminoids; came up after clearing whilst four native species; *Podocarpus elongatus* (tree), *Berkheya rigida* (herb), *Platycaulos callistachyus* (graminoid), *Oxalis pes-caprae* (geophyte) failed to return following clearing. The following plant species important for birds increased in abundance after clearing: shrubs: *Diospyros glabra* (native) and *Ricinus communis* var. *communis* (alien), graminoids: *Bromus diandrus* (alien), *Avena fatua* (alien), *Lolium multiflorum* (alien), *Bromus catharticus* (alien); geophytes: *Zantedeschia aethiopica* (native) and forbs: *Picris echioides* (alien), *Rumex crispus* (alien), *Sisymbrium capense* (alien) and *Solanum nigrum* (alien) (Table S3.3).

3.3.2. Effect of habitat characteristics on bird assemblages

Invasion status, adjacent land use and canopy cover contributed significantly to bird species richness and abundance (Table 3.1). Interactions between invasion condition x canopy cover and interactions between plant species richness x canopy cover had a significant influence on bird species richness ($P < 0.05$ for all interactions, GLM). Two interaction terms; season x plant species richness and surrounding land-use x plant species richness ($P < 0.05$, for all interactions, GLM) were significant determinants of bird abundance.

Table 3.1. Results from main effects analysis from a generalised linear model showing variables that had significant effect on bird species richness and bird abundance.

Independent variable	Bird species richness				Bird abundance			
	Est.	Std. Error	z-value	<i>P</i>	Est.	Std. Error	z-value	<i>P</i>
Invasion condition	0.754	0.241	3.119	0.001	0.823	0.165	5.000	<0.001
Adjacent landuse	0.393	0.122	3.198	0.001	0.325	0.081	4.609	0.001
Canopy cover (%)	-0.008	0.003	-2.654	0.008	-0.010	0.002	-4.449	0.001
Season	-0.275	0.151	-1.821	0.069	0.182	0.102	-1.781	0.075
Plant species richness	0.009	0.016	0.551	0.581	0.002	0.010	0.181	0.856
Plants with fruits	0.009	0.018	0.470	0.639	0.021	0.013	1.718	0.086
Plants with flowers	0.014	0.014	1.032	0.302	0.002	0.009	-0.164	0.870
Plants with seeds	-0.039	0.024	-1.619	0.105	-0.006	0.016	-0.390	0.696
Maximum plant height (m)	-0.033	0.037	-0.912	0.361	-0.008	0.026	-0.320	0.749

3.3.3. Response of bird assemblages to *Eucalyptus camaldulensis* clearing

A total of 2049 birds from 53 species (26 species in invaded sites, 41 species in cleared sites and 42 species in near-pristine sites) were recorded. Invaded sites had significantly lower bird species richness ($F = -7.03$, $df = 179$, $P < 0.01$) while there was no significant difference in bird species richness between cleared and near-pristine sites ($F = -0.28$, $df = 179$, $P = 0.78$) (Fig. 3.4 a). There was no increase in bird richness with time since clearing ($F = 0.655$, $df = 3$, $P = 0.6$; Fig. 3.4 b). Bird abundance was significantly lower in invaded sites ($F = -6.3$, $df = 179$, $P < 0.01$) whilst cleared and near-pristine sites were similar ($F = 0.28$, $df = 179$, $P = 0.78$; Fig. 3.4 c). There was no increase in bird abundance with time since clearing ($F = 1.95$, $df = 3$, $P = 0.13$; Fig. 3.4 d).

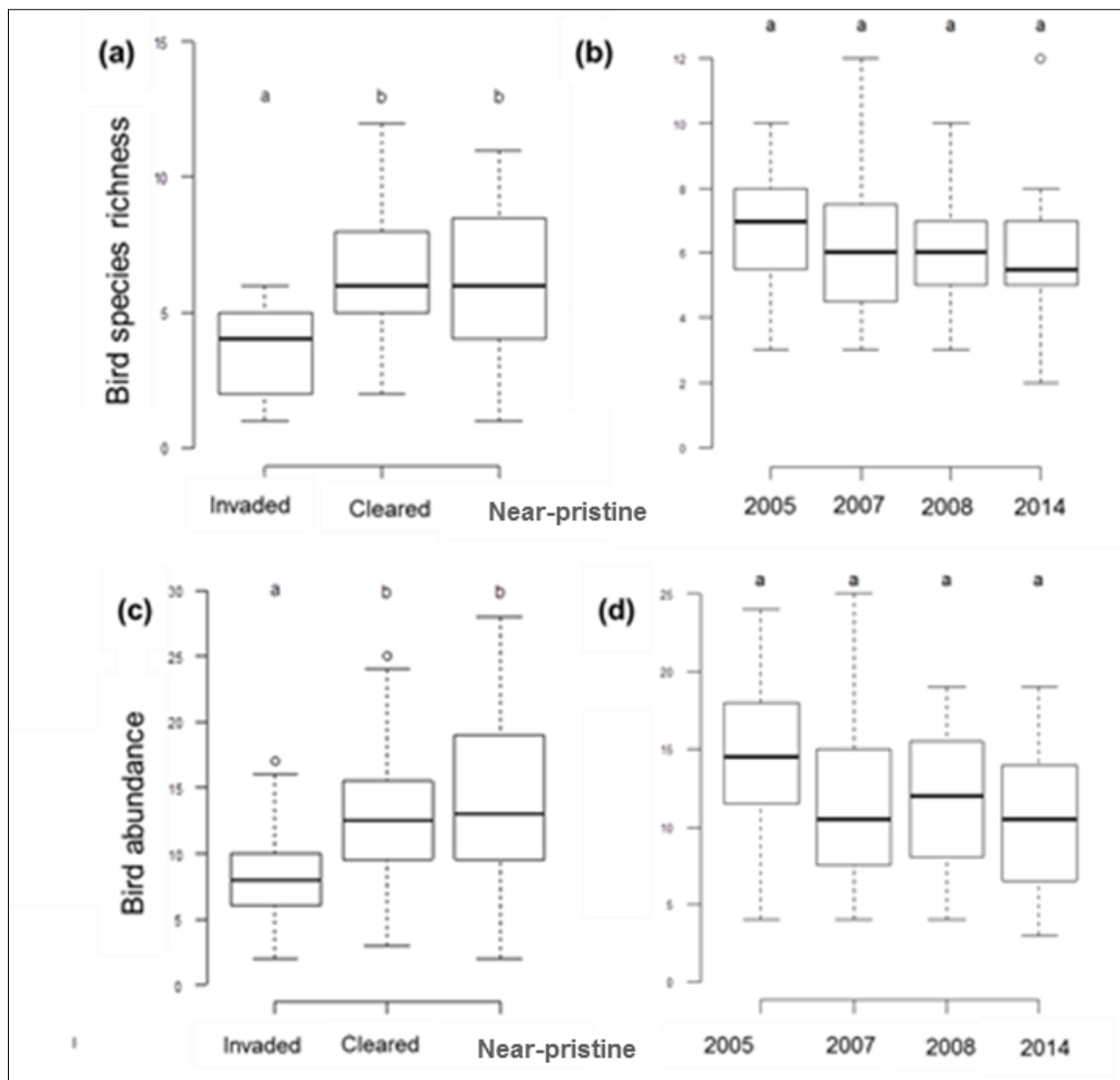


Figure 3.4. Comparison of (a) bird species richness in invaded, cleared and near-pristine sites; (b) bird species richness over time since clearing; (c) bird abundance in invaded, cleared and near-pristine sites and (d) bird abundance over time since clearing. Box plots display median, 25th and 75th percentiles, and data range. Open circles indicate outliers.

Frugivores, nectarivores and herbivores had largely recovered ten years after clearing although their abundance was still lower than in near-pristine sites (Fig. 3.5). Ten of the 18 bird species lost due to the *Eucalyptus camaldulensis* invasion had returned a decade after clearing. There were nine new species, most of them carnivores, that were making use of cleared sites. Insectivores, granivores, omnivores and carnivores showed a gradual increase in species returning after clearing but some species are still missing (Fig. 3.5). Raptor species are still missing a decade after clearing, with only the Yellow-billed Kite returning.

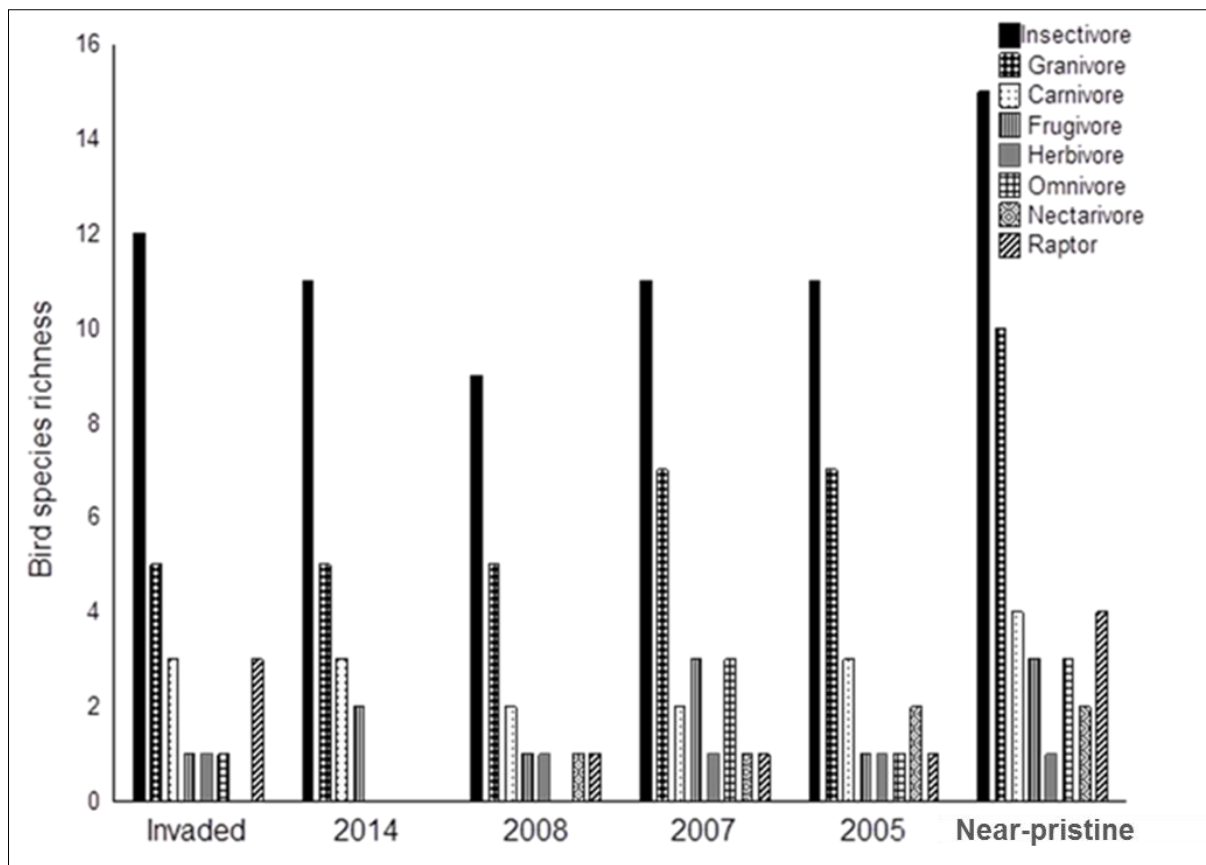


Figure 3.5. Bird species richness per feeding guild in sites cleared in different years, compared to invaded and near-pristine.

3.4. Discussion

Clearing of *Eucalyptus camaldulensis* from the riparian habitat of the Berg River was sufficient to aid avifaunal recovery with only a few species still missing. Bird assemblages improve post-clearing with little changes with the passage of time. Results show that, except for raptors, all bird guilds show a progressive increase in bird species richness post-clearing. Consistent with other studies from Mediterranean ecosystems, our results show a link between plant and bird assemblage recovery (Herrando & Brotons 2002; De la Montana *et al.* 2006; Chalmandrier *et al.* 2013). However, ten years after clearing, both plant and bird assemblages are not fully recovered, indicating the need for a longer time interval for assemblages to recover to near-pristine levels. Recovery could be accelerated by intervention through the re-introduction of specific keystone native plant species by means of sowing seeds and/or planting native trees (Heleno *et al.* 2010).

Alien trees have fast recruitment rates and out-compete indigenous vegetation resulting in monospecific stands with altered species compositions and structural diversity (Schwartz *et al.* 2006; Hulme & Bremner 2006; Le Maitre *et al.* 2011). Results from this study show that invasion

by *Eucalyptus camaldulensis* mostly suppressed the growth of native trees (Fig. 3.3). This result concurs with findings from other studies in the fynbos biome where native species richness and abundance changed due to invasion by *Acacia*, *Eucalyptus* and *Pinus* species (Richardson & van Wilgen 2004; Holmes *et al.* 2005). These negative effects on vegetation in turn negatively affect bird assemblages; with specialist guilds such as nectarivores being most affected (see Dean *et al.* 2002; Greve *et al.* 2011; Rogers & Chown 2013). In this study invasion by *E. camaldulensis* resulted in a drastic reduction in frugivores and the complete exclusion of nectarivores. This effect on frugivores and nectarivores, which are important seed dispersers and pollinators, consequently affects the perpetuation of a number of native plants (Rebello 1987; Knight 1988).

Clearing releases resources such as water, nutrients, space and sunlight for other species, facilitating revegetation from soil seedbanks and from propagules dispersed from remnant native plants in surrounding areas (also see Morris *et al.* 2008; Reinecke *et al.* 2008; Ruwanda *et al.* 2013a, b). Revegetation by native plants directly influences the recovery of associated faunal assemblages through the increase of habitat and food (Procheş *et al.* 2008; Simberloff *et al.* 2010; Holland-Clift *et al.* 2011). This is confirmed by other studies in Mediterranean regions which have reported that bird succession after a disturbance relied largely on vegetation regeneration (Herrando *et al.* 2002; Chalmandrier *et al.* 2013). The return of generalist bird species occurs first followed by specialists as their food resources are gradually restored (Herrando *et al.* 2002; Chalmandrier *et al.* 2013). Furthermore, Chalmandrier *et al.* (2013) show that fynbos specialist bird species such as nectar feeders, that rely on specific food resources, only return when these resources are restored. In our study, the return of nectar feeding birds in eight-year old sites can be attributed to the recovery or return of plant species such as *Melianthus major*. Whether an increase in nectarivores effectively translates into the restoration of the bird-pollinated plant guild remains to be tested. Despite this, the restoration of this ecosystem function (pollination) is important for ecosystem resilience of the restored habitat (Handel 1997).

Following clearing, frugivores also recover in bird richness although bird abundance is still low when compared to near-pristine sites. Recovery of this bird guild could be attributed to an increase in the abundance of fleshy fruit-bearing plants after clearing. The increase in the abundance of species such as *Kiggelaria africana*, *Olea europea* subsp. *africana* can also be attributed to dispersal from remnant vegetation and surrounding areas. *K. africana* is most abundant in cleared sites where it occurs as clumps of mature trees. We speculate that *K. africana* is one of the few species that survived invasion, since it is a shade tolerant species and

requires overstorey vegetation to establish (Vosse *et al.* 2008). *Podocarpus elongatus*, a fleshy-fruit bearing species also beneficial to frugivores, is still absent ten years post clearing and this could partly explain the low abundance of frugivores. According to Galatowitsch and Richardson (2005), *P. elongatus* is also absent in soil seedbanks but this species could benefit from the occurrence of other trees in restored sites which are used as perches by seed dispersing birds. The return of *Rhus angustifolia* after clearing could be attributed to bird dispersal but it may also be a reflection of their ability to persist in the soil-stored seedbanks (Pretorius *et al.* 2008).

Plant species richness increased following clearing but there is a high occurrence of alien plants in cleared sites. However, it is important to note that native plant species richness in cleared sites is similar to that of near-pristine sites. The high level of alien plants in cleared sites is due to an array of forb and graminoid species (Galatowitsch & Richardson 2005; Morris *et al.* 2008; Ruwanza *et al.* 2013a, b). Ruwanza *et al.* (2013a) speculate high cover of alien forbs and graminoids to have negative effects and sets back the recovery of native plants, and trees in particular, but whether that is true needs to be determined. Some alien herbaceous species have been demonstrated to invade following alien tree clearing (Reinecke *et al.* 2008). However, forb species that occur in our cleared sites might not be a threat since they are pioneer species as well as non-invasive annuals which have a short life-span and die off at the end of the growing season.

Increase of forb and graminoid species due to high nutrient levels have also been reported following removal of nitrogen-fixing invasive *Acacia* species in terrestrial systems (Yelenik *et al.* 2004). In their study on vegetation response following *E. camaldulensis* clearing from the Berg River riparian system, Ruwanza *et al.* (2013a) attribute the increase in forb and graminoid plant species to a possible increase in soil fertility from decayed *Eucalyptus* plant litter. Since the number of years needed for nutrient levels to subside and return to pre-invasion levels following *E. camaldulensis* invasion is unknown we also speculate that the soils in cleared sites along the Berg River are still nutrient-enriched ten years after clearing hence promoting the growth of herbs and graminoids. In addition, Mentis and Ellery (1994) agree with Sousa (1984) that the response of herbs and graminoids is quickest in primary succession after a disturbance hence the dominance of these life forms in our cleared sites is expected.

Granivores also increased in species richness and bird abundance over time as a direct response to a gradual increase in graminoid plants over time since clearing. Although no new granivore species were recorded, the Red-eyed Dove and the Sweet Waxbill which are forest granivore species are still absent, pointing to the absence of large overstorey trees in cleared

sites. Apart from wind and water activity, birds are also important for seed dispersal of grass species which might be detrimental to ecosystem recovery since some grass species such as *Pennisetum clandestinum*, *Avena fatua*, *Lolium multiflorum* and *Bromus diandrus* recorded in our study, are known to be invasive (Milton 2004). Therefore, although the presence of birds as seed dispersers could be valuable to accelerate restoration, their occurrence can also facilitate invasion by alien plants (Heleno *et al.* 2010).

Invasive alien plants can have a direct effect on aerial feeding birds through depletion of invertebrate communities (Samways *et al.* 1996, Samways & Taylor 2004) and indirectly as an obstacle when hunting for insects (Avarind *et al.* 2010). There is an upward trend in the species richness and abundance of insectivores over time following clearing but assemblages have not fully recovered to near-pristine levels. Although our study did not look into the recovery of insect populations, our results are consistent with Magoba and Samways (2010) who reported an increase in invertebrate populations following alien plant clearing from a riparian habitat. The absence of large overstorey trees in cleared sites could explain the absence of the Paradise Flycatcher which is a forest species that feeds by gleaning insects off leaves.

Six new bird species make use of cleared sites most of them being carnivores with fish and large invertebrates as the main food source. In their study, Samways and Sharratt (2010) concur with Magoba and Samways (2010) that river water quality is depleted when alien trees are present and this reduces fish and water invertebrate diversity. In the above-mentioned studies, water quality improves and consequently fish and invertebrate populations recover approximately seven years after invasive alien plant clearing and subsequent reestablishment of native trees. Similarly in our study the Malachite Kingfisher, White-breasted Cormorant and the Reed Cormorant returned in seven year-old cleared sites.

Only one raptor species, the Yellow-billed Kite returned to cleared sites. The absence of other raptors such as the African Fish Eagle, the Jackal Buzzard and the Steppe Buzzard could be due to absence of large native trees used by these species for nesting, roosting and as a vantage point for hunting (Ewbank 2000; Suddjian 2004; Cilliers & Siebert 2012). The Yellow-billed Kite is present early on after clearing. The absence of a closed canopy creates an ideal open hunting ground for the Yellow-billed Kite consisting largely of seed producing grasses which attract rodents and smaller birds which make up part of their prey (Hockey *et al.* 2005).

Natural recovery of native plant species, through native soil-stored seedbanks and recruitment from remnant natural vegetation, is the ideal and desirable outcome of restoration projects.

Passive restoration saves costs, limits recolonisation by alien plants and points to ultimate recovery from invasion (Blanchard & Holmes 2008; Morris *et al.* 2008). However, failure of native plants to naturally re-establish without further activities such as sowing native seeds and planting native trees have been encountered (Galatowitsch & Richardson 2005; Harms & Hiebert 2006). Vegetation recovery can fail when biotic and abiotic thresholds have been surpassed and unsuitable conditions for germination of dispersed seeds from nearby areas exist (Galatowitsch & Richardson 2005; Holmes *et al.* 2005; Vosse *et al.* 2008; Ruwanza *et al.* 2013a).

Observations from our study suggest that several bird species fail to return to cleared sites due to the protracted recovery of native plant species, hence the absence of a suitable habitat and food resources. Some native trees and shrubs such as *Olea europea* subsp. *africana*, *Kiggelaria Africana*, *Diospyros glabra*, *Melianthus major* and *Rhus angustifolia* have returned but still occur at low abundance. An increase in the abundance of these species could enhance recovery of vegetation diversity and structure and the return of associated bird assemblages (Pretorius *et al.* 2008; Ruwanza *et al.* 2013b). The situation could also be improved by active intervention through the introduction of riparian tree species such as *Podocarpus elongatus*, *Brabejum stellatifolium*, *Cunonia capensis* and *Salix mucronata* subsp. *hirsuta* together with shrubs such as *Euclea tomentosa* and *Leonotis leonurus* that are critical for nectarivores and frugivores. *Anthospermum*, *Stoebe*, *Athanasia*, *Berzelia*, *Protea* and *Leucadendron* species are known to be better pioneers and can be introduced as a means to suppress alien herbs (Pretorius *et al.* 2008). We also advocate active re-introduction of selected keystone species, such as *P. elongatus*, *B. stellatifolium* and *C. capensis* on the wet banks and in closed areas as these species can not tolerate open and dry areas (Blanchard & Holmes 2008). Other than also being important for birds, these species recruit easily from seeds and/or cuttings and hence easily germinate and establish (Holmes *et al.* 2008; Ruwanza *et al.* 2013b). In addition, these species are locally available along the riparian area of the Berg River (Ruwanza *et al.* 2013b). Broadhurst *et al.* (2008) suggest that efforts should first be put to source these species selected for re-introduction from the surrounding landscape to avoid genetic pollution. Sourcing these species locally would also save money which is the most limiting resource in restoration projects. The introduction of these species to cleared sites will benefit bird assemblages through an increase in food supply, nesting and perching sites and the overall recovery of assemblages.

3.5. Acknowledgements

We acknowledge funding from the DST-NRF Centre of Excellence for Invasion Biology and the Working for Water Programme through their collaborative research project on “Integrated

Management of invasive alien species in South Africa". We also acknowledge funding from the National Research Foundation (Grant 87843). We thank the landowners who allowed access to their properties and Michelle Slabber for fieldwork assistance.

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Supplementary tables

Table S3.1. Invasion condition, site size and coordinates for the study sites.

Invasion condition	Coordinates	Size (ha)
Invaded	-33.58638; 18.91365	2.4
Invaded	-33.56855; 18.93551	11.8
Invaded	-33.44900; 18.95300	4.6
Invaded	-33.45368; 18.94190	3.7
Invaded	-33.58700; 18.94600	12.5
Cleared	-33.46430; 18.94110	5.0
Cleared	-33.44611; 18.95672	4.6
Cleared	-33.49380; 18.93650	5.2
Cleared	-33.45970; 18.95130	4.5
Cleared	-33.46430; 18.94400	2.3
Cleared	-33.48920; 18.93420	3.9
Near-pristine	-33.47300; 18.93900	5.6
Near-pristine	-33.45800; 18.95000	3.8
Near-pristine	-33.44700; 18.9560	1.6
Near-pristine	-33.47500; 18.93800	5.1

Table S3.2: Common names, scientific names and feeding guilds for all bird species observed in this study.

Common name*	Scientific name*	Feeding guild*	Food source	Bird weight*
Bar-throated Apalis	<i>Apalis thoracica</i>	Insectivore	Insects, spiders, seeds and fruit	9- 13g
Cape Batis	<i>Batis capensis</i>	Insectivore	Small insects	10-14g
Yellow Bishop	<i>Euplectes afer</i>	Granivore	Seeds and insects	25-50g
Southern Boubou	<i>Laniarius ferrugineus</i>	Insectivore	Invertebrates, reptiles, mice, fruit	45-68g
Cape Bulbul	<i>Pycnonotus capensis</i>	Frugivore	Fruits, seeds, nectar, insects	30-46g
Cape Bunting	<i>Emberiza capensis</i>	Granivore	Fruits, seeds, buds, insects	17-27g
Jackal Buzzard	<i>Buteo rufofuscus</i>	Raptor	Small mammals, reptiles, birds, frogs, insects	900-1700g
Steppe Buzzard	<i>Buteo vulpinus</i>	Raptor	Small mammals, reptiles, birds, frogs	510-700g
Cape Canary	<i>Serinus canicollis</i>	Granivore	Seeds, fruit, flower, insects	12-22g
Forest Canary	<i>Crithagra scotops</i>	Granivore	Seeds, fruit, flowers, leaves, insects	12- 20g
Yellow Canary	<i>Crithagra flaviventris</i>	Granivore	Seeds and small fruit	17-18g
Cape-Robin Chat	<i>Cossypha caffra</i>	Insectivore	Insects, other invertebrates, fruit	23-38g
Ant-eating Chat	<i>Myrmecocichla formicivora</i>	Insectivore	Insects, other invertebrates, fruit	40-60g
Leviallant's Cisticolla	<i>Cisticola tinniens</i>	Insectivore	Insects	12g
Reed Cormorant	<i>Phalacrocorax africanus</i>	Carnivore	Fish, invertebrates	450-650g

White-breasted Cormorant	<i>Phalacrocorax lucidus</i>	Carnivore	Fish	1800-3200g
Pied Crow	<i>Corvus albus</i>	Omnivore	Fruit, seeds, insects, amphibians	410-610g
Diderick's Cuckoo	<i>Chrysococcyx caprius</i>	Insectivore	Insects, other invertebrates	35g
Red-eyed Dove	<i>Streptopelia semitorquata</i>	Granivore	Seeds, bulbs, insects	190-300g
Ring-necked Dove	<i>Streptopelia capicola</i>	Granivore	Seeds, nectar, invertebrates	100-160g
Fork-tailed Drongo	<i>Dicrurus ludwigii</i>	Insectivore	Insects, small birds, reptiles, fish	38-55g
African black Duck	<i>Anas sparsa</i>	Omnivore	Plants, invertebrates	780-1280g
Maccoa Duck	<i>Oxyura maccoa</i>	Carnivore	Aquatic invertebrates	550-800g
African Fish Eagle	<i>Haliaeetus vocifer</i>	Raptor	Fish, birds, reptiles, carrion	2000-3800g
Fiscal Flycatcher	<i>Sigelus silens</i>	Insectivore	Insects, grasshoppers	26g
Paradise Flycatcher	<i>Terpsiphone viridis</i>	Insectivore	Insects	11-17g
Common Fiscal	<i>Lanius collaris</i>	Carnivore	Invertebrates, reptiles, birds, frogs	25-50g
Helmeted Guinea Egyptian Goose	<i>Numida meleagris</i> <i>Alopochen aegyptiaca</i>	Omnivore Herbivore	Bulbs, leaves, seeds Grass, seeds	800-1500-3500g
Black-headed Heron	<i>Ardea melanocephala</i>	Carnivore	Small mammals, birds, reptiles, invertebrates	1200-1900g
Hadedda Ibis	<i>Bostrychia hagedash</i>	Carnivore	Insects, worms, other invertebrates	1000-1100g
Yellow-billed Kite	<i>Milvus aegyptius</i>	Raptor	Insects, reptiles, frogs, small mammals, birds	570-700g

Brown-throated Martin	<i>Riparia paludicola</i>	Insectivore	Insects	10-16g
Red-faced Mousebird	<i>Urocolius indicus</i>	Frugivore	Fruits, flowers, leaves, nectar	40-70g
Speckled Mousebird	<i>Colius striatus</i>	Frugivore	Fruits, buds, leaves, nectar	35-65g
African Pipit	<i>Anthus cinnamomeus</i>	Insectivore	Insects	22-28g
Karoo Prinia	<i>Prinia maculosa</i>	Insectivore	Insects and spiders	8-11g
Three-banded Plover	<i>Charadrius tricollaris</i>	Carnivore	Insects, worms, crustaceans	28-45g
Common Quail	<i>Cortunix cortunix</i>	Granivore	Seeds, bulbs, roots, leaves	80-115g
Streaky-headed Seedeater	<i>Crithagra gularis</i>	Granivore	Seed, fruit flowers, buds, nectar, insects	12-25g
Cape Sparrow	<i>Passer melanurus</i>	Granivore	Seed, fruit flowers, buds, nectar, insects	22-36g
House Sparrow	<i>Passer domesticus</i>	Granivore	Seeds, fruit, buds, nectar, insects	22-30g
Malachite Sunbird	<i>Nectarinia famosa</i>	Nectarivore	Nectar, insects, spiders	11-25g
Southern Double-Collared Sunbird	<i>Cinnyris afer</i>	Nectarivore	Nectar, insects, spiders	6-10g
Cape Pendulline- Tit	<i>Anthoscopus minutus</i>	Insectivore	Insects, larvae, spiders beetles	7.5g
Cape Wagtail	<i>Motacilla capensis</i>	Insectivore	Insects, small fish, reptiles, tadpoles	18-24g
African Reed Warbler	<i>Acrocephalus baeticatus</i>	Insectivore	Insects	8-14g
Cape Weaver	<i>Ploceus capensis</i>	Insectivore	Insects, fruits, buds	54g
Southern Masked-Weaver	<i>Ploceus velatus</i>	Insectivore	Insects, fruit, nectar, seeds	30-44g

Cape White-Eye	<i>Zosterops virens</i>	Insectivore	Insects, fruit, nectar	8-12g
Pin-tailed Whydah	<i>Vidua macroura</i>	Granivore	Seeds, insects	13-17g

*Feeding guild classification, bird names and bird weight measurements based on Hockey *et al.* (2005) and birds were categorised basing on the following main food component making up its foraging substrate (main food component makes up to 50% of total food consumed): Carnivore- Large arthropods and vertebrates; Frugivore- Fleshy fruits; Granivore-Seeds or grain; Herbivore- Plant material; Insectivore- Insects; Nectarivore-Nectar; Raptor- Large vertebrates and small mammals; Omnivore- 2 or more of the above.

Table S3.3: Plant species occurring across invaded, cleared and near-pristine sites along the Berg River in the Western Cape of South Africa. Values presented in this table are calculated species specific occurrences. Values show the frequency (%) of a specific species in the different treatments with (-) indicating the absence of a species.

Plant species names	Occurrence (abundance per invasion)			Status*	Growth form*
	Invaded	Cleared	Near-pristine		
<i>Acacia karoo</i>	1.33	-	5	Native	Tree
<i>Acacia mearnsii</i>	26	1.66	-	Alien	Tree
<i>Acacia saligna</i>	2.66	-	-	Alien	Tree
<i>Asparagus rubicundus</i>	-	1.11	-	Native	Shrub
<i>Athanasia trifurcata</i>	-	1.11	3.33	Native	Shrub
<i>Avena fatua</i>	4	9.4	5	Alien	Graminoid
<i>Berkheya rigida</i>	-	-	2.5	Native	Herb
<i>Bromus catharticus</i>	-	11.66	15.83	Alien	Graminoid
<i>Bromus diandrus</i>	0.66	1.11	1.66	Alien	Graminoid
<i>Chasmanthe aethiopica</i>	2.66	-	-	Native	Graminoid
<i>Chenopodium ambrosioides</i>	-	0.55	-	Alien	Herb
<i>Cissampelos capensis</i>	-	0.55	-	Native	Vine
<i>Cucumis myriocarpus</i>	-	2	-	Native	Herb
<i>Cynodon dactylon</i>	17.33	15.55	3.33	Alien	Graminoid
<i>Cyperus esculentus</i>	0.66	-	-	Native	Graminoid
<i>Diospyros glabra</i>	2.66	10	8.33	Native	Shrub
<i>Echium plantagineum</i>	-	0.55	0.83	Alien	Herb
<i>Eliocharis limosa</i>	4	-	-	Native	Graminoid
<i>Eucalyptus camaldulensis</i>	84	-	-	Alien	Tree
<i>Halleria elliptica</i>	-	1.11	-	Native	Shrub
<i>Hypochoeris radicata</i>	-	0.55	-	Alien	Herb

<i>Inula graveolens</i>	-	1.11	-	Native	Herb
<i>Jasminum glaucum</i>	-	-	0.83	Native	Vine
<i>Juncus effusus</i>	1.33	-	-	Native	Graminoid
<i>Kiggelaria africana</i>	-	11	25	Native	Tree
<i>Lactuca serriola</i>	1.33	4.4	5.83	Alien	Herb
<i>Lepidium africanum</i>	-	0.55	1.66	Native	Herb
<i>Limonium sinuatum</i>	0.66	2.22	-	Native	Herb
<i>Lolium multiflorum</i>	2	36.11	15	Alien	Graminoid
<i>Melianthus major</i>	-	1.11	-	Native	Shrub
<i>Nothoscordum gracile</i>	0.66	-	-	Native	Geophyte
<i>Olea europaea subsp. africana</i>	-	5	11.66	Native	Tree
<i>Oxalis pes-caprae</i>	0.66	-	12.5	Native	Graminoid
<i>Pennisetum clandestinum</i>	21.33	1.11	-	Alien	Graminoid
<i>Picris echioides</i>	2	12.77	8.33	Alien	Herb
<i>Platycoulos callystachys</i>	-	-	1.66	Native	Graminoid
<i>Poa annua</i>	1.33	1.11	10	Alien	Graminoid
<i>Podocarpus elongatus</i>	-	-	34.16	Native	Tree
<i>Rhus angustifolia</i>	-	6.66	11.66	Native	Shrub
<i>Ricinus communis var. communis</i>	2	9.4	-	Alien	Shrub
<i>Rubus cuneifolius</i>	5.33	2.22	-	Alien	Shrub
<i>Rumex crispus</i>	0.66	5	1.66	Alien	Herb
<i>Senecio hamilifolius</i>	-	3.33	-	Native	Herb
<i>Sisymbrium capense</i>	0.66	1.11	0.83	Native	Herb
<i>Solanum mauritianum</i>	1.33	-	-	Alien	Tree
<i>Solanum nigrum</i>	0.66	2.22	-	Alien	Herb

<i>Solanum pseudocapsicum</i>	-	10	-	Alien	Shrub
<i>Sonchus asper</i>	-	0.55	-	Alien	Herb
<i>Sonchus oleraceus</i>	-	5	3.33	Alien	Herb
<i>Tradescantia fluminensis</i>	0.66	-	-	Alien	Herb
<i>Xanthium strumarum</i>	0.66	-	-	Alien	Herb
<i>Zantedeschia aethiopica</i>	3.33	18.88	18.33	Native	Geophyte

*Plant species status classification (alien or native) based on Goldblatt and Manning (2000) and Bromilow (2010)

*Plant growth form classification: trees, shrubs, forbs, graminoids (grasses, sedges and restioids - reed-like plants that belong to the *Restionaceae* or Cape Reed family), geophytes (perennial plants that are propagated by buds on underground bulbs, tubers or corms), and vines (creeping and climbing plants) based on Goldblatt & Manning (2000).

Supplementary figures

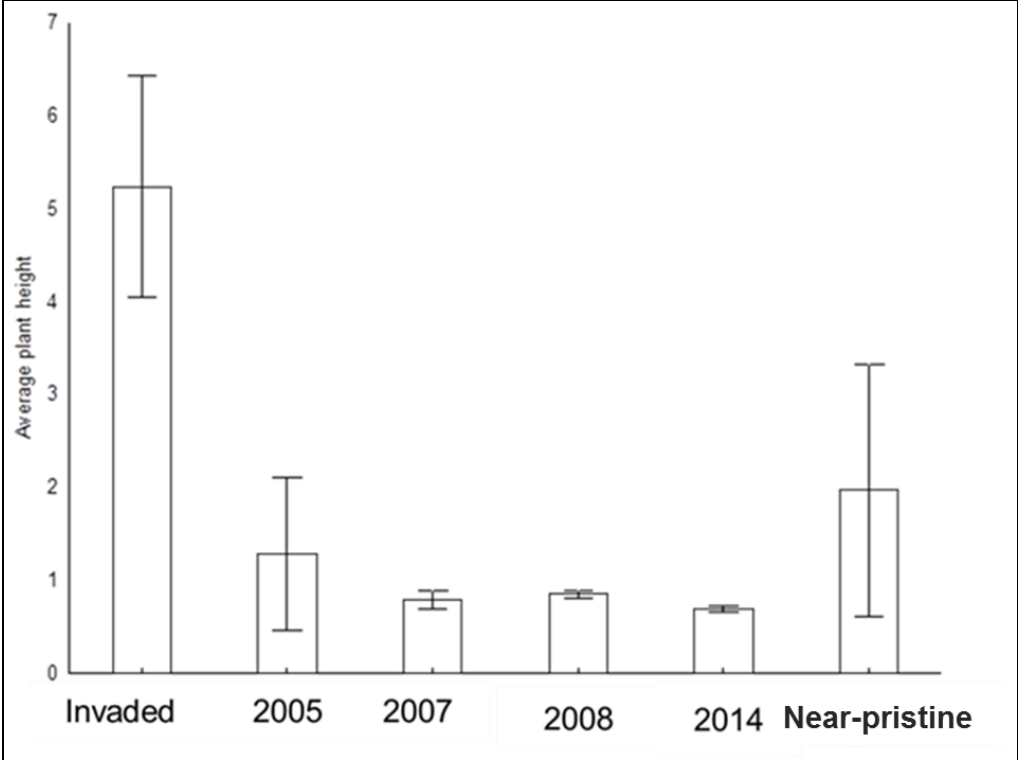


Figure S3.1. Average plant height in sites of different invasion conditions.

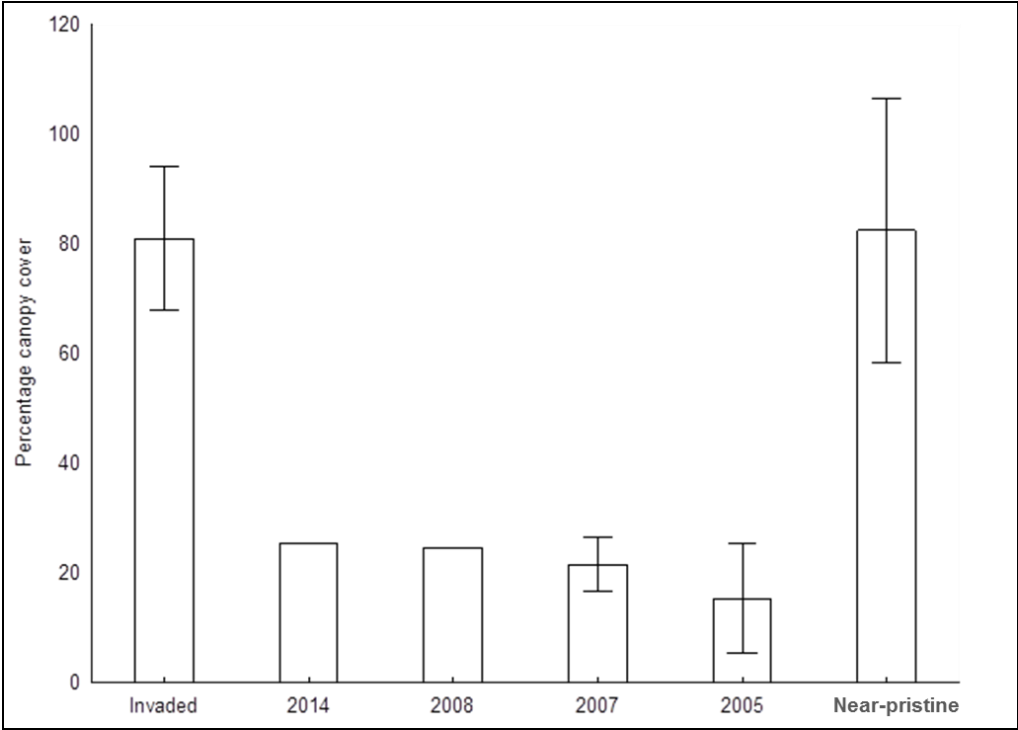


Figure S3.2. Percentage canopy cover in sites of different invasion conditions.

CHAPTER FOUR

IT IS ALL ABOUT LAND USE: RESPONSE OF BIRD ASSEMBLAGES TO INVASIVE ALIEN PLANT COVER AT DIFFERENT SPATIAL SCALES

Abstract

The spread of invasive alien plants coupled with commercial agriculture and urbanisation has variable impacts on natural habitats and biodiversity. Transformation of pristine areas by invasive alien plants can either be beneficial or detrimental to bird assemblages. I hypothesise that the response of bird assemblages depends on both the intensity of the disturbance and on the spatial scale. At two different spatial scales, I expect the highest bird species richness at moderate invasive alien plant (IAP) cover, as is predicted by the intermediate disturbance hypothesis (IDH). To test this hypothesis, I overlaid the second South African Bird Atlas Project (SABAP2) data with the National Invasive Alien Plant Survey (NIAPS) data to analyse impacts of IAP cover on bird assemblages at the local and landscape scales in the Cape Floristic Region (CFR). At both spatial scales, there was an increase in bird species richness and bird abundance as IAP cover increased, but the IDH only holds for bird species richness at a landscape scale. This is largely driven by the raptors, nectarivorous and insectivorous guilds. Although IAP cover influences bird assemblages at the landscape scale, urban and agricultural land uses are more important than IAP cover. At a local scale the highest bird diversity occurred at the highest level of IAP cover. This illustrates that whether the IDH holds true for the response of bird assemblages' to IAP depends on the spatial scale and bird guild.

Key words: Bird assemblages, Cape Floristic Region, Intermediate disturbance hypothesis, Land use, Nectarivore, Plant invasions, Spatial scale.

4.1. Introduction

Human activities have resulted in the loss of biological diversity through habitat transformation (Chapin *et al.* 2000; Pimm & Raven 2000). Commercial farming (Stoate *et al.* 2001; Foley *et al.* 2005) and urbanisation (Czech *et al.* 2000; Chace & Walsh 2006) are the most prominent land uses that fragment or destroy natural habitats. In addition to agriculture and urbanisation, the spread of invasive alien plants (IAP) have largely contributed to habitat alteration with variable effects on native fauna (Samways & Taylor 2004; Tallamy 2004; Rogers & Chown 2013). Low to moderate habitat transformation may benefit bird assemblages and increase species richness by promoting habitat complexity and increasing available niches (Balmford *et al.* 2001; Rogers & Chown 2013). At the same time, areas that have experienced high levels of transformation from intense farming, dense urbanisation and high IAP cover, support depauperate bird assemblages (Savard *et al.* 2000; Marzluff & Ewing 2001; Waltert *et al.* 2003). This illustrates that, although human-induced habitat changes in general impact negatively on biodiversity, bird assemblages exhibit losses, gains or no

response depending on the intensity of transformation, affected ecosystem and bird guild (Gjerde & Sætersdal 1997; Sogge *et al.* 2008).

Most studies tend to focus on effects of invasive alien plants at localised scales (Richardson & van Wilgen 2004), but the effects of invasive alien plants are known to extend from the plot to the landscape scale (Sax & Gaines 2003; Pauchard & Shea 2006; Gaertner *et al.* 2009). Thus the response of bird assemblages might largely depend on the scale of study (Wiens 1989; Wu *et al.* 2000). Sax and Gaines (2003) define the local scale to be an area larger than a single plot and measuring from a few square metres to a few hectares in extent. The presence of birds at this small spatial scale largely depends on floristic heterogeneity (Fleishman *et al.* 2009), but alien plants are known to dominate and change floristic compositions leading to homogenised plant communities (Vilà *et al.* 2011; Tererai *et al.* 2013; chapter 3). Since the response of bird assemblages to habitat changes is often linked to floristic heterogeneity and their specialisation on certain food substrates (Fleishman *et al.* 2009; Grass *et al.* 2013; chapter 2 & 3), habitat specialists, such as nectarivore and frugivore species are lost (chapter 2 & 3).

At a larger, landscape spatial scale (Sax & Gaines 2003), other variables such as habitat size and structure become important (Rotenberry 1985; Armstrong & Van Hensbergen 1994). This includes surrounding land uses such as nature reserves, the presence of a river or wetland, agricultural areas or built-up areas that all influence the bird diversity across the landscape (Hockey & Midgley 2009). This variety of habitats increases both food and structural resources, which are important for resident species, leads to an increase in both bird species richness and abundance (Fairbanks 2004; Mitchell *et al.* 2005). Bird species richness indicates the variety of resources present in a habitat whereas bird abundance provides a reflection of the quality of available resources in a habitat (Betts *et al.* 2008; Lloyd 2008). Thus, although transformed habitats may be suitable for birds, they might not have the potential to sustain assemblages over time, limiting their long-term potential in biodiversity conservation (Boal & Mannan 1999; Battin 2004). Generally, the potential of transformed habitats to sustain diverse bird assemblages depends on the capacity of different species to make use of available resources, failure of which leads to displacement of specialist species and increase in generalists (Rogers & Chown 2013).

Nel *et al.* (2004) postulate that most of South Africa's natural ecosystems are under threat of transformation from IAP. By the year 2000, up to 10 million ha, or 8.28% of South Africa's surface area had already been affected (Le Maitre *et al.* 2000; Le Maitre *et al.* 2002; Richardson & van Wilgen 2004). The bulk of invasive species of concern are woody plants whose presence has a pronounced effect on already limited water resources (Le Maitre *et al.* 2002; Richardson & van Wilgen 2004). Effects of invasion also include the displacement of

native plants and the reduction of plant richness and diversity, resulting in monospecific stands of closed canopy woodlands (Richardson *et al.* 1989; Tererai *et al.* 2013). The loss of floristic and structural diversity due to alien plant invasions is an important change which has cascading effects on animal communities (Richardson *et al.* 2004). It is essential to understand response of bird assemblages to these changes at different intensities and spatial scales.

According to van Wilgen *et al.* (2016), only 19% of the surface area of the Cape Floristic Region (CFR) is part of the protected areas network, making biodiversity conservation beyond protected area boundaries important. The CFR is an area of high endemism with over 9000 plant species (Goldblatt & Manning 2002) and the spread of IAP in this region is a cause of concern. Impacts of IAP on biodiversity have been well studied in South Africa with most of the research having been done in the CFR (Richardson & van Wilgen 2004). Although the scale of study is acknowledged to influence impacts of IAP, studies to quantify impacts of plant invasion at scales beyond the small spatial scale (plot level) are scarce (Richardson & van Wilgen 2004). There is also limited information on the effects of IAP on animal communities with the bulk of studies focusing on native plants (Samways *et al.* 1996). Thus, in this study I extend beyond chapter 2 and 3 of this thesis where I quantified impacts of IAP on bird assemblages at a plot scale. I use the second South African Bird Atlas Project data (SABAP2; Harebottle *et al.* 2010) and data on IAP cover for different invasive alien plants (NIAPS; Kotzé *et al.* 2010) for the western extent of the CFR. I use these datasets to quantify the impacts of IAP on bird assemblages at the local and landscape scale. I also aim to determine if bird assemblages exhibit the same patterns as shown at the plot scale (chapter 2 & 3).

According to Connell (1978), the intermediate disturbance hypothesis (IDH) predicts that a moderately disturbed habitat will have higher species diversity when compared to areas with lower or higher levels of disturbance. Based on the IDH, I hypothesise that at the landscape scale, moderate levels of habitat transformation through IAP, agriculture and urbanisation will result in an increase in bird species richness and bird abundance due to an increase in the available niches (Connell 1978; McDonnell & Pickett 1990; Fairbanks *et al.* 2000). However, as habitat transformation continues to increase, heterogeneity is suppressed and the number of niches will also decline, and so will bird richness and abundance (Fig. 4.1 a, slightly adapted IDH graph and based on results from chapter 2 & 3). I also expect that at the landscape scale, other land uses might become more important and result in different responses (Fig. 4.1 b, c). Based on chapter 2 and 3, I expect that bird assemblages at the local scale will respond to IAP cover according to the IDH (Fig. 4.1 a). Out of the bird feeding guilds, I hypothesise that raptors at the landscape scale will follow the IDH and increase in species richness due to an increase IAP cover.

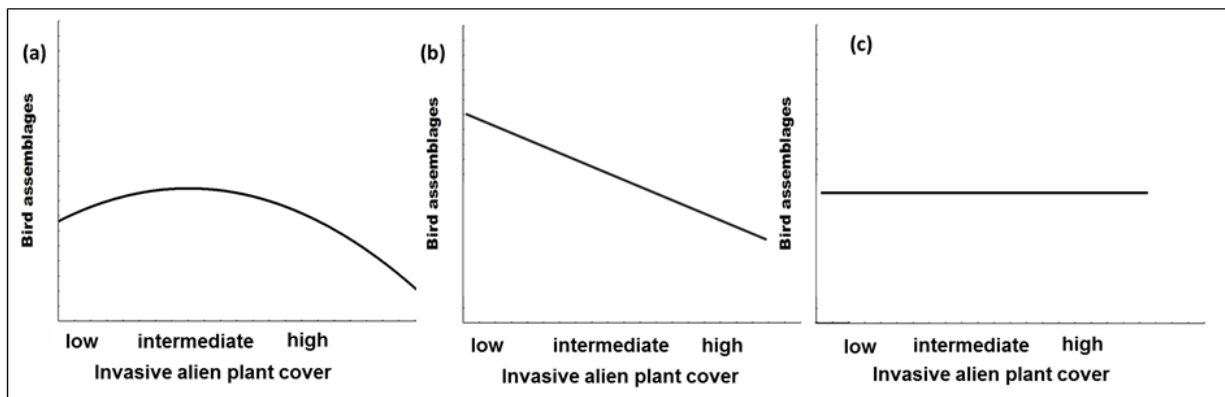


Figure 4.1. Potential responses of bird assemblages (bird species richness and bird abundance) to habitat transformation from invasive alien plants at both the local and landscape scale; (a) response consistent with the intermediate disturbance hypothesis (IDH) where more diversity occurs at moderate invasive alien plant (IAP) cover, (b) a negative correlation with bird assemblages decreasing with increase in IAP cover (Rogers & Chown 2013) and (c) no effect in bird assemblages with increase in IAP cover (Shanahan *et al.* 2011).

Increase in IAP cover translates into an increase in structure, available habitat and seed production by aliens which will result in an increase prey populations (e.g. rodents). However, I expect raptor species richness to decline as IAP cover continues to increase. I also expect generalist species such as granivores and insectivores to follow the IDH and increase in species richness at both spatial scales due to an increase in food resources but declining in species richness as IAP cover continues to increase. Lastly, at both the local and landscape scale I expect that habitat specialists such as nectarivores will be negatively affected by the presence of invasive alien plants and that they will decrease in species richness (Fig. 4.1 b). Hence my aim is to determine the interaction between IAP cover and bird species richness, abundance and feeding guilds at different spatial scales.

4.2. Methods

Data on invasive alien plant (IAP) cover (ha) was obtained from the National Invasive Alien Plant Survey (NIAPS; Koetzé *et al.* 2010) while data on bird distribution, bird species richness and bird abundance was obtained from the second South African Bird Atlas Project (SABAP2; Harebottle *et al.* 2010). Since the unit of spatial measurement for SABAP2 is the pentad (8.0 km by 7.6 km), NIAPS data which is available at a finer scale (250 m by 250 m) had to be scaled up to correspond to the bird data. For this study, data from the CFR was selected from both datasets for analyses (Fig. 4.2). Apart from being the same area where the plot scale study (chapter 2 & 3) was carried out, the CFR was chosen because it is both an area of high endemism but at the same time is highly invaded (Richardson & van Wilgen 2004). Linking the NIAPS and SABAP2 datasets to the same geo-referenced system using ArcMap 10.1 enabled exploring and quantifying the impacts of invasive alien plants on fynbos birds' richness and abundance to be done.

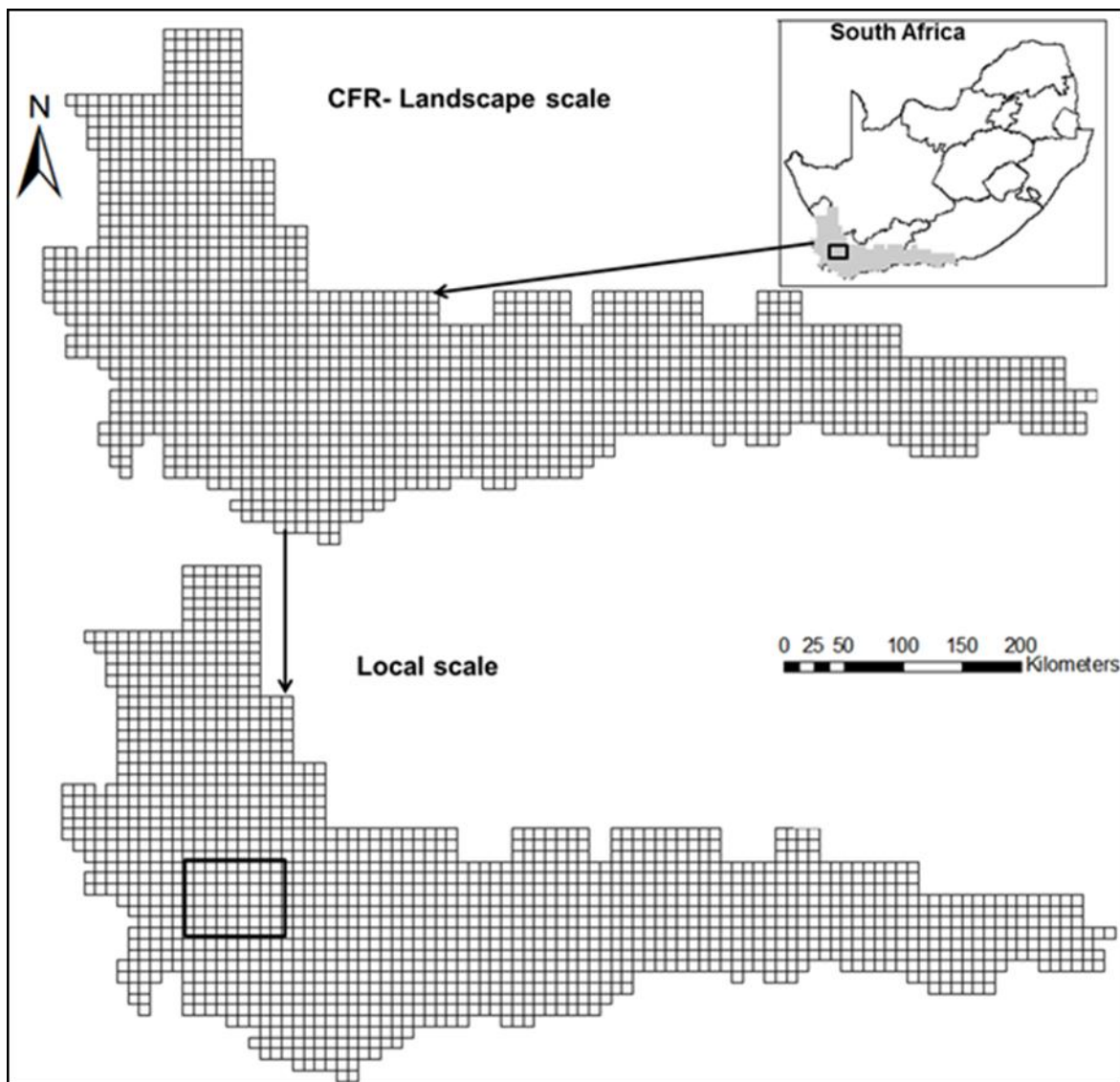


Figure 4.2. Map of the study region showing the spatial extent of pentads at the local and landscape scales.

4.2.1. Invasive alien plant data

The data on invasive alien plant (IAP) cover include records for 32 alien plant species, mostly trees and shrubs, at the quaternary catchment level (Kotzé *et al.* 2010). Arid bioregions and some land cover classes such as mining were excluded from the survey (Kotze pers. comm.), but did not affect our analyses, since these land cover classes are rare or absent in the CFR. Plant data provide an average density (AVEdens) value for each 250 m by 250 m grid, that is the average density of all the invasive alien species combined (Kotzé *et al.* 2010). Since the data on invasive alien plants were available at 250 m by 250 m, scaling up to the pentad level resulted in a patchwork of average density values in a pentad. AVEdens value and area (m²) covered per pentad were used to calculate condensed area (ha), a value inclusive of average density and area covered per pentad. Condensed area (ha) per pentad was subsequently used for all analyses.

Pentads with up to 80% of the total surface area covered with ocean and/or urban areas were excluded from analyses without affecting the results. Pentads were extracted from the remaining data to represent the local scale, that is the area surrounding (and including) the study sites for the plot study in chapter 2 and 3 (n = 39) and the landscape scale which is data for the CFR (n = 789).

4.2.2. Bird data

Data on birds were extracted from the second South African Bird Atlas Project (SABAP2) (2007 to July 2016) and was obtained from the Avian Demographic Unit (ADU), University of Cape Town. The spatial resolution for the surveys is a pentad covering five minutes of latitude by five minutes of longitude (5' × 5') which is approximately 8.0 km × 8.0 km (Harebottle *et al.* 2010). SABAP2 is a national citizen survey carried out in 17 444 pentads covering South Africa, Lesotho and Swaziland. Temporal resolution is a 5-day period where presence/absence data of identified bird species are recorded (Harebottle *et al.* 2010). This data also provides a measure of bird abundance based on the reporting rates: which is the proportion of checklists on which a species is recorded out of the total number of checklists submitted for that specific pentad (Fairbanks *et al.* 2002). This measure gives a rough estimate of abundance since observers do not count actual number of birds seen (Harrison & Navarro 1994).

All pentads with less than four species checklists received were removed from the dataset since as a rule of thumb, pentads with fewer than four species cards are poorly sampled (Harrison *et al.* 1997). Thus, pentads for the landscape scale only include those covering mostly the western part of the CFR, since a number of pentads on the eastern part had incomplete bird records. Pentads for the local scale include the area surrounding (and including) the study sites for the plot study in chapter 2 and 3. Bird species were grouped into eight feeding guilds namely; insectivores, nectarivores, frugivores, carnivores, raptors, herbivores, granivores and omnivores (Hockey *et al.* 2005).

4.2.3. Data analyses

A polynomial function (Statistica version 13; StatSoft Inc. 2016) was used to detect non-linear relationships between IAP cover and the response variables namely; bird species richness, bird abundance and the different feeding guilds (Legendre & Legendre 1998). A generalised linear model with Poisson distribution and a log-linked function was then used to determine the extent to which other land uses affected bird assemblages at large spatial scales. The following predictors on bird assemblages were included in the analysis, namely: invasive alien plant (IAP) cover (condensed ha), percentage agriculture and percent urban areas. At the local scale, urban areas are not included in the generalised linear model since there are only very small town communities embedded within predominantly farming areas at

this scale (pers. obs.). To assess for spatial patterns between plant and bird data, ArcMap 10.1 was used to overlay the two datasets using the Projected Coordinate System: WGS Albers and the Geographic Coordinate System: CGS WGS 1984.

4.3. Results

4.3.1. Landscape scale

Bird species richness increased gradually with increase in invasive alien plant (IAP) but started decreasing when IAP cover went beyond 100 condensed hectares per pentad (Fig. 4.3 a), but this was not significant (Polynomial $r = 0.06$, $N = 797$, $P = 0.09$; Fig. 4.3 (a)). Bird abundance decreased and then increased with an increase in IAP cover per pentad (Polynomial $r = -0.04$, $N = 797$, $P = 0.00$; Fig. 4.3 (b)).

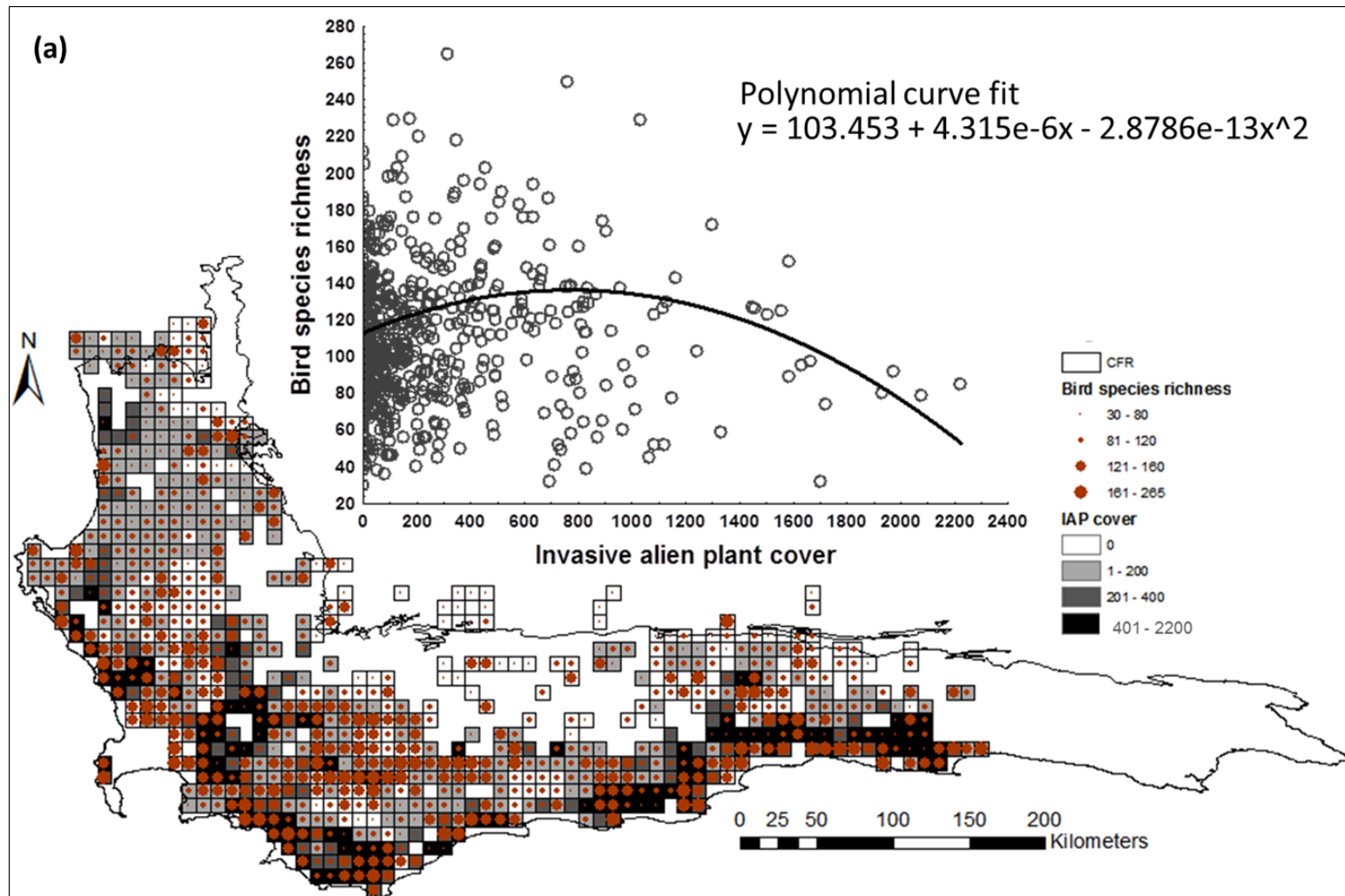


Figure 4.3 (a) Spatial and graphic (insert) presentation of bird species richness against invasive alien plant cover (condensed hectares per pentad) at the landscape scale. A polynomial fit was included in the graph to show the response pattern of bird species richness to invasive alien plant cover.

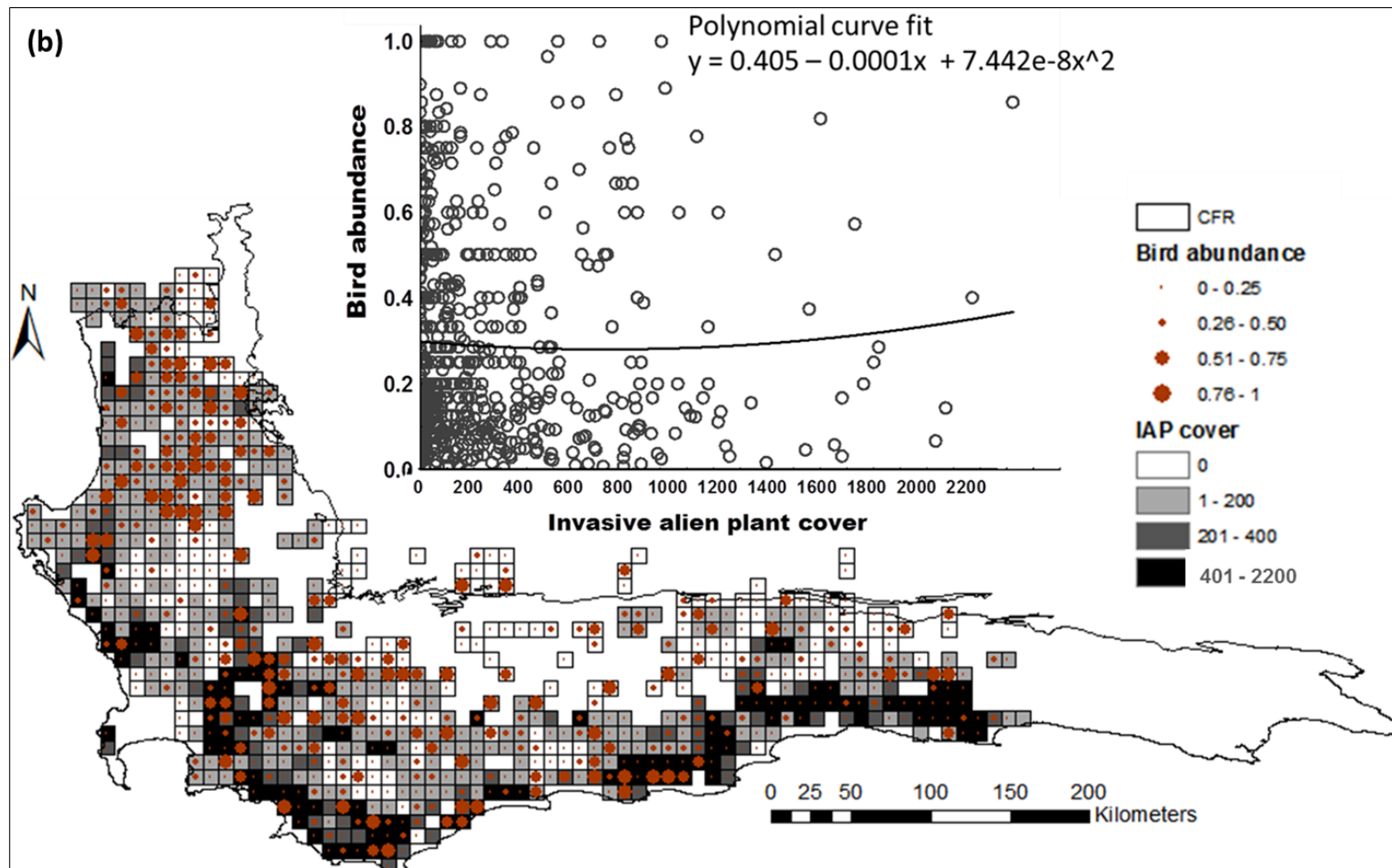


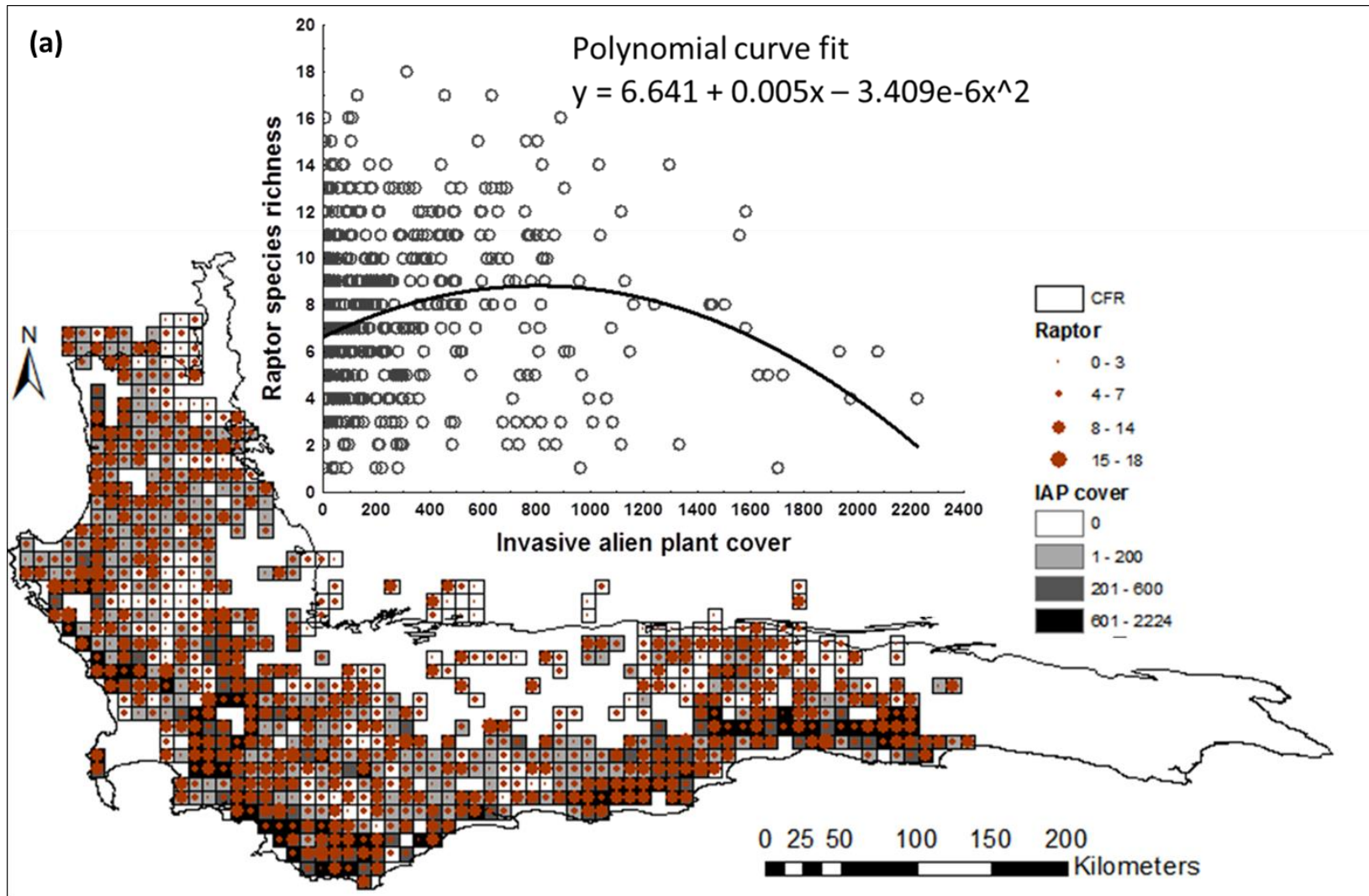
Figure 4.3 (b) Spatial and graphic (insert) presentation of bird abundance against invasive alien plant cover (condensed hectares per pentad) at the landscape scale. A polynomial fit was included in the graph to show the response pattern of bird abundance to invasive alien plant cover.

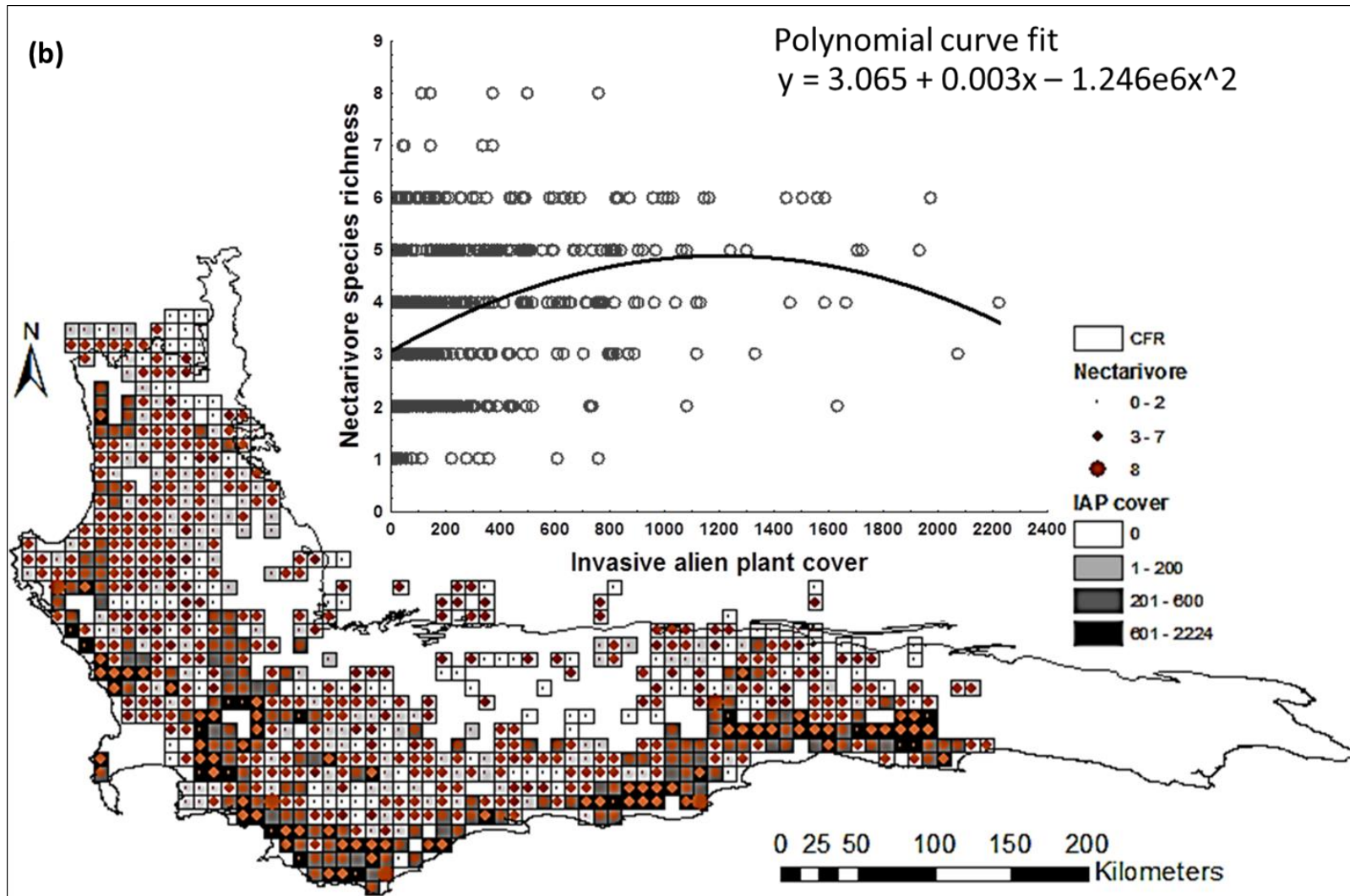
Urban (Wald statistic = 834.9, N = 797, $P = 0.00$) and agricultural areas (Wald statistic = 417.6, N = 797, $P = 0.00$) largely explained bird species richness (Table 4.1).

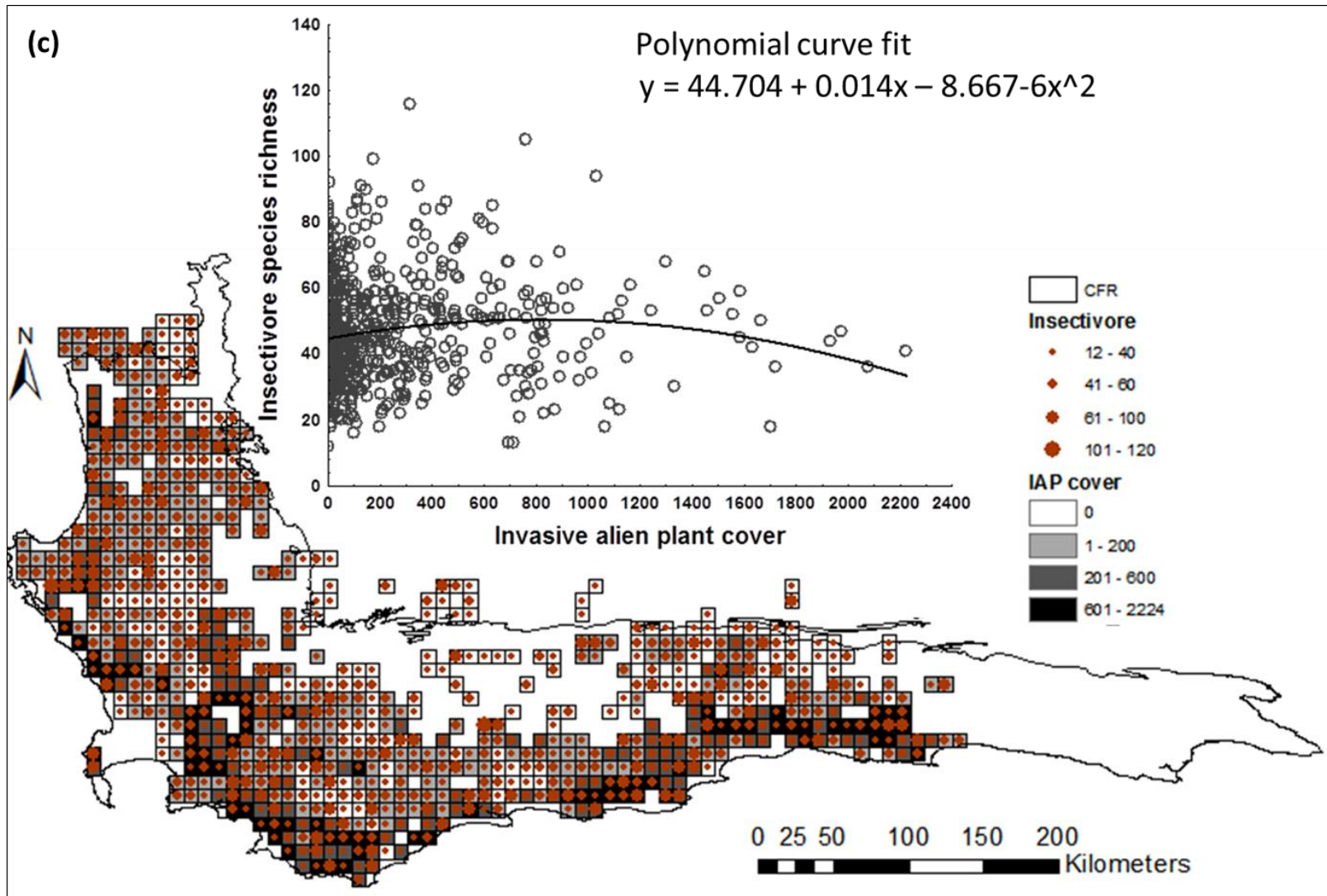
Table 4.1. Results from the generalised linear model showing the response of bird assemblages to invasive alien plant cover, agriculture and urban areas at the landscape and local scale. Only small towns occur at the local scale hence the exclusion of urban areas as a predictor variable in the analysis.

Response	Predictor variables							
	IAP (ha)		Agriculture		Urban areas			
Landscape scale (N = 797)	Wald Stat.	P	Wald Stat.	P	Wald Stat.	P		
Bird species richness	48.30	0.00	417.6	0.00	834.9	0.00		
Bird abundance	0.07	0.79	3.26	0.07	3.37	0.0		
Nectarivores	26.44	0.00	14.85	0.00	4.98	0.02		
Frugivores	2.28	0.13	4.42	0.03	10.87	0.00		
Raptors	35.77	0.00	130.99	0.00	101.76	0.00		
Insectivores	16.35	0.00	72.25	0.00	226.00	0.00		
Granivores	6.28	0.01	26.50	0.00	27.02	0.00		
Local scale (N = 39)								
Bird species richness	75.49	0.00	385.8	0.00				
Bird abundance	37.56	0.00	21.37	0.00				
Nectarivores	0.70	0.40	0.56	0.45				
Frugivores	1.57	0.21	0.43	0.51				
Raptors	1.17	0.27	3.08	0.07				
Insectivores	2.13	0.14	6.89	0.00				
Granivores	1.18	0.27	3.08	0.07				

There was a significant increase in species richness of raptors (Polynomial $r = 0.11$, $N = 797$, $P = 0.00$; Fig. 4.4 (a)), nectarivores (Polynomial $r = 0.32$, $N = 797$, $P = 0.00$; Fig. 4.4 (b)), and insectivores (Polynomial $r = 0.07$, $N = 797$, $P = 0.05$; Fig. 4.4 (c)) as IAP cover increased. Dynamics of these guilds followed the intermediate disturbance hypothesis (IDH) (Fig. 4.4 (a), (b), and (c) insert). Granivores significantly decreased in species richness as IAP cover increased (Polynomial $r = -0.10$, $N = 797$, $P = 0.00$; Fig. 4.4 (d)) and did not follow the IDH (Fig. 4.4 (d) insert). Although the pattern shown by bird feeding guilds were mainly influenced by agriculture, the presence of invasive alien plants also had an effect (Table 4.1).







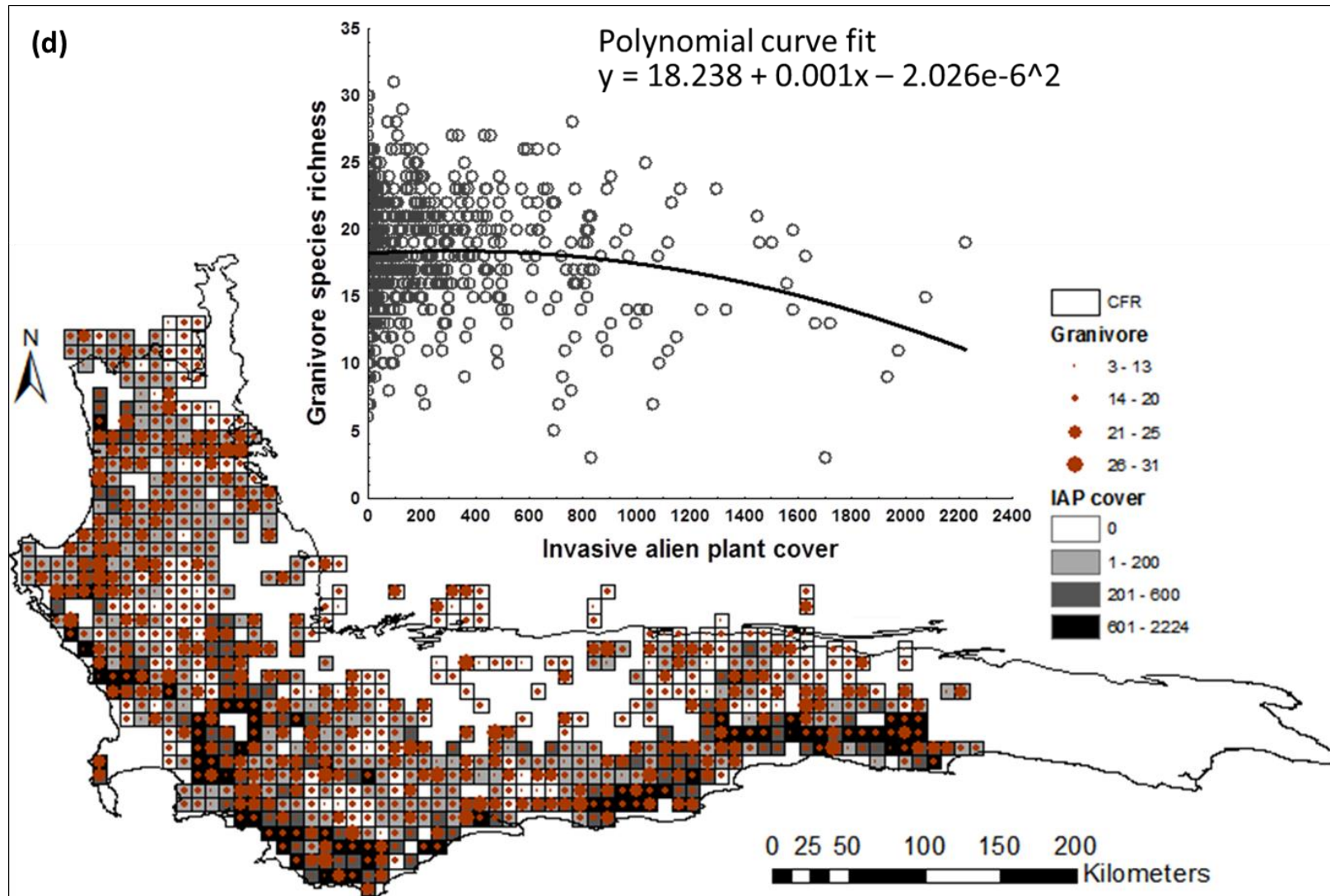


Figure 4.4. Spatial and graphic (insert) presentation of (a) raptor, (b) nectarivore, (c) insectivore and (d) granivore species richness against invasive alien plant cover (condensed hectares per pentad) at the landscape scale. In all graphs a polynomial fit was included to show the response pattern of bird assemblages to invasive alien plant cover.

4.3.2. Local scale

There was a significant increase in bird abundance with increase in invasive alien plant (IAP) cover (Polynomial $r = 0.35$, $N = 39$, $P = 0.00$; Fig. 4.5 (b)) but not for bird species richness (Polynomial $r = 0.00$, $N = 39$, $P = 0.99$; Fig 4.5 (a)). Both bird species richness and bird abundance continued to increase with the highest diversity attained at the highest IAP cover (Fig. 4.5 (a), (b) insert).

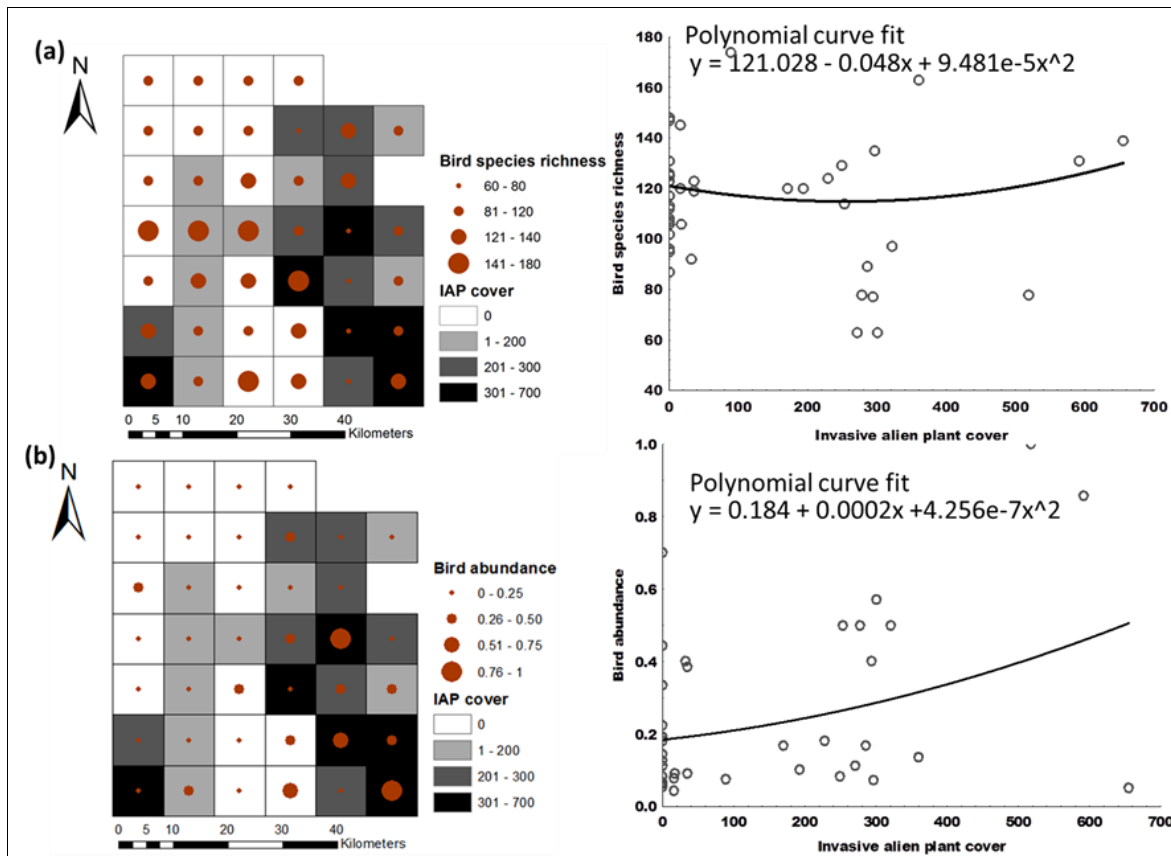


Figure 4. 5. Spatial and graphic presentation at the local scale of (a) bird species richness and (b) bird abundance against invasive alien plant cover (condensed hectares per pentad). In both graphs a polynomial fit was included to show the response pattern of bird assemblages to invasive alien plant cover.

Agriculture was more important for bird richness whilst IAP cover was important for bird abundance (Table 4.1). Although there was an increase in species richness for the guilds with increase in IAP cover, the increase was not significant for raptors (Polynomial $r = -0.04$, $N = 39$, $P = 0.79$; Fig. 4.6 a), insectivores (Polynomial $r = -0.06$, $N = 39$, $P = 0.72$; Fig. 4.6 c) and granivores (Polynomial $r = -0.05$, $N = 39$, $P = 0.78$; Fig. 4.6 d). Raptors, insectivores and granivores had lowest species richness at intermediate levels of IAP cover (Fig. 4.6 a, c and d insert).

While IAP cover had an effect on the responses shown by the different guilds, the proportion of land under agricultural land use was more important than IAP cover for raptors, insectivores and granivores (Table 4.1).

Nectar feeders showed a significant increase in species richness at low invasive alien plant cover (Polynomial $r = 0.63$, $N = 39$, $P = 0.00$; Fig. 4.6 b) but a decline in richness begins with increase in cover (Fig. 4.6 b insert). Invasive alien plants largely drive this pattern for nectar feeders (Table 4.1).

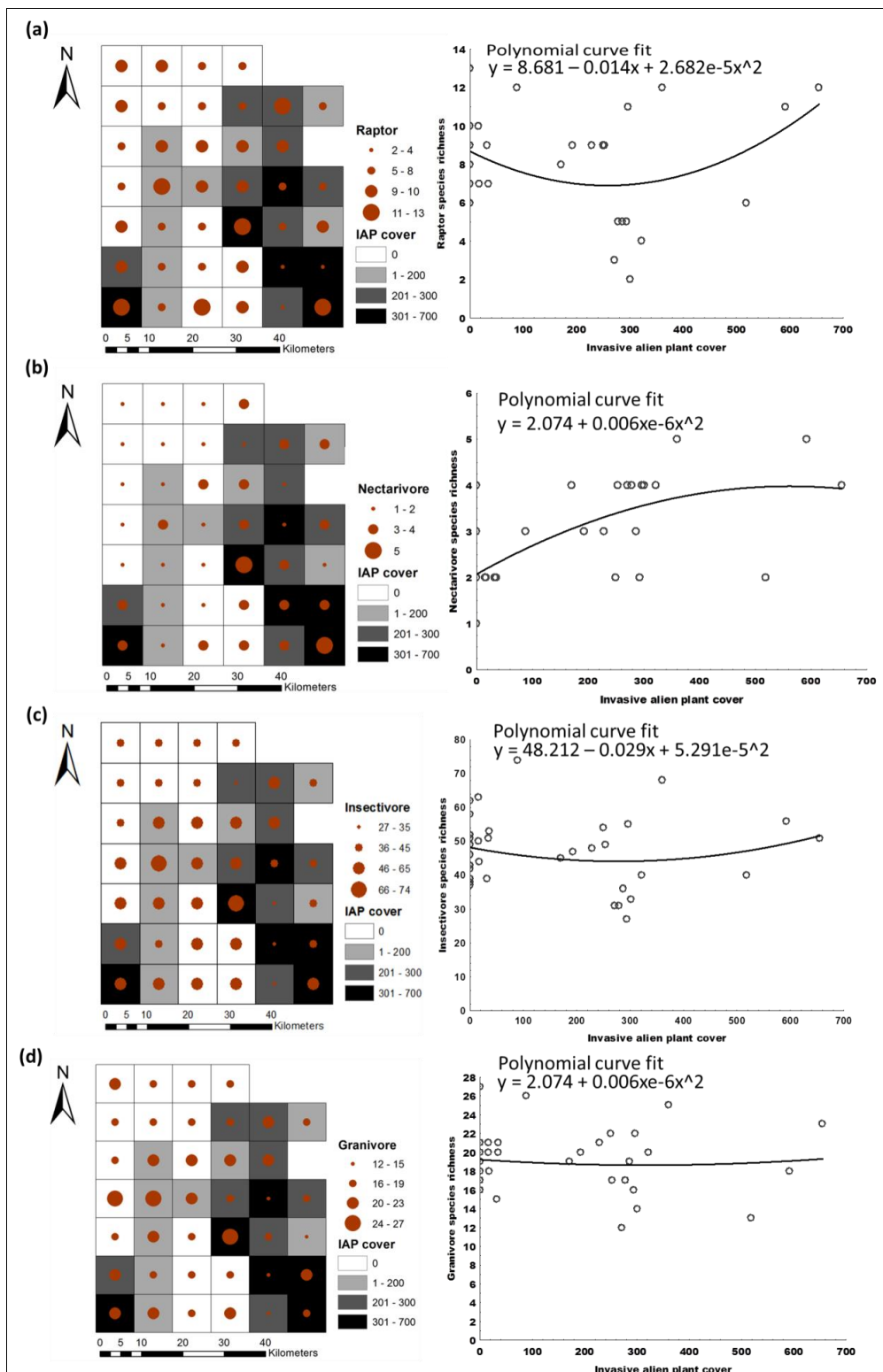


Figure 4.6. Spatial and graphic presentation of (a) raptor, (b) nectarivore, (c) insectivore and (d) granivore species richness against invasive alien plant cover (condensed hectares per pentad). In all graphs a polynomial fit was included to show the response pattern of bird assemblages to invasive alien plant cover.

4.4. Discussion

4.4.1. Landscape scale

The response of bird species richness to invasive alien plant (IAP) cover is consistent with the intermediate disturbance hypothesis (Connell 1978). Bird species richness increases with an increase in area covered by alien plants and peaks at moderate levels of invasion but eventually declines as IAP cover continues to increase. These results are consistent with results from other studies where bird species diversity was highest at intermediate levels of habitat disturbance from human land use (Lance & Phinney 2001; Lepezyk *et al.* 2008; Powell *et al.* 2011; Seress & Liker 2015 but see Fairbanks *et al.* 2002). At very low levels of invasion, bird species richness remains low and beyond 1000 condensed hectares per pentad, the high levels of IAP cover have adverse effects and leads to a reduction in bird species richness (Fig. 4.3 a insert). At intermediate levels of disturbance, a variety of habitats occur together (McKinney 2002) and the presence of alien plants probably complements available resources from native plant species. At this stage, IAP might benefit birds by creating heterogeneous and structurally more complex habitats, thereby opening up new niches (McKinney 2002). Higher levels of disturbance decrease habitat productivity and available resources and present challenges and threats to avifauna which results in low species richness (Boal & Mannan 1999).

Invasive alien plant (IAP) cover affects bird species richness, but urbanisation and agriculture are more important variables driving patterns in bird species richness. Consistent with other studies, areas with moderate levels of transformation such as the edge of urban areas support higher levels of biodiversity (McKinney 2002; Chace & Walsh 2006). The existence of urban areas corresponds with an increase in human population size, complex land uses and increases in plant species introductions, thereby enhancing habitat heterogeneity and encouraging occupancy (Patausso 2007; Chang *et al.* 2016). Landscaping and the occurrence of green spaces (e.g. parks) in urban areas also lead to an increase in plant diversity and structural complexity; consequently offering more foraging, nesting sites and protection from predators and all these factors attract more bird species (Fairbanks 2004; Chang *et al.* 2016). However, at high levels of urban development such as the urban core and in intensive agricultural areas, bird species richness decreases due to low plant species richness, lower vegetation complexity (Shochat *et al.* 2006), and a lack of suitable food resources (Chase & Walsh 2006).

Patterns in bird abundance are not consistent with the intermediate disturbance hypothesis (IDH). Although there is a peak in species richness at intermediate levels of disturbance suggesting habitat complexity and an increase in resources, bird abundance declines at intermediate levels of disturbance (Betts *et al.* 2008). Some low quality habitats such as urbanised environments may attract high bird diversity due to signs of habitat suitability such

as nesting sites but at the same time being an ecological trap concealing death causing elements such as disease (Boal & Mannan 1999; Battin 2004). Apart from the effects of IAP cover on bird abundance, urban areas are the most important variable predicting bird abundance. The low effect of IAP on bird abundance at intermediate levels of disturbance might suggest an inferior habitat availability despite the high species richness recorded. This raises the possibility that human transformed habitats provide short-term refugia for avifauna without assurance of populations remaining viable over long time periods (Battin 2004; Rodewald *et al.* 2011).

Species richness of raptors increased with an increase in IAP cover but a further increase in alien cover results in a drop in species richness. The CFR contains vegetation types that are highly diverse but with low structural complexity (Chalmandrier *et al.* 2013). At intermediate levels of IAP cover, there is an increase in habitat structure, providing raptors with elevated points which they use for hunting, more nesting and more roosting sites (Hajzlerova & Reif 2014). This increase in important resources translates into an increase in raptor species richness. However, at very high levels of IAP cover, the importance of alien plants to raptors decreases. The importance of invasive alien plants to raptors is evident when a few tall alien trees occur in a mosaic of native plants, but this effect is removed when the landscape is dominated by invasive alien plants (chapter 2 & 3).

Agricultural activities largely predict raptor bird species richness at landscape scale. Agriculture has led to the establishment of road networks, powerlines and artificial water impoundments (Meunier *et al.* 1999). These artificial habitats might provide additional nesting sites and easy accessibility to prey (Meunier *et al.* 1999). Management activities in agricultural areas such as leaving grass covering field margins also encourage habitation by small mammals which are prey to raptors (Meunier *et al.* 1999). However, intensification of agriculture may reduce benefits to raptors through high pesticide use and increase in monocultures which decrease habitat quality and heterogeneity thereby reducing raptor species richness (Cardador *et al.* 2010). Despite the effects of habitat transformation through agriculture and IAP cover, not all raptor species have been affected in the same way. Several species of falcons, eagles and kestrels have managed to adapt and are tolerant of man-made habitats (Cardador *et al.* 2010). At the same time, some species have home ranges extending into pristine areas beyond farm boundaries and do not need cultivated areas to meet all their ecological requirements (Cardador *et al.* 2010).

Invasive alien plant (IAP) cover is highly positively related to nectarivore species richness and patterns show evidence for the IDH (Fig. 4.4 b). The peak in richness at intermediate levels of IAP cover could be explained if the invasive alien plants offer a source of nectar (Le Roux *et al.* 2010; Geerts & Pauw 2013). However nectarivore species richness declines as

invasion increases beyond a threshold cover. This reduction in species numbers is consistent with results from other studies in the CFR where a low number of nectarivore or a complete lack was reported in habitats invaded by alien plant species (Fraser & Crowe 1990; Greve *et al.* 2011; Rogers & Chown 2013; chapter 2 & 3).

Granivores show a weak support for IDH and this response was not expected since some alien plants provide an abundant source of seeds and hence food for granivores (Fraser & Crowe 1989; Rogers & Chown 2013). The response was also not expected since other studies show granivores to be generalist species, which are not highly sensitive to habitat change (McKinney & Lockwood 2001; Fairbanks *et al.* 2002; Fairbanks 2004). However, the explanation for a decrease in granivore species could be based on what has been reported elsewhere that some native granivores avoid seed produced by alien plants (Dudgeon & Corlett 2004; Leven & Corlett 2004).

An increase in insectivore bird species in invaded stands was reported by Fraser and Crowe (1989) and Rogers and Chown (2013). Increase in insectivore numbers was attributed to a mix of alien and native vegetation (Fraser & Crowe 1989). The results of Fraser and Crowe (1989) suggest that at intermediate levels of IAP cover within stands of native vegetation, insectivores benefit from the increase in available insects. As IAP cover continues to rise, the diversity of herbivorous insects is reduced (Samways & Taylor 2004; Gerber *et al.* 2008) with direct negative impacts on insect feeding birds (Procheş *et al.* 2008). In other instances, dense invasions become barriers to insectivores when they hunt for prey (Avarind *et al.* 2010) leading to a decrease in insectivores in invaded areas. Thus, several other factors apart from IAP cover influence the occurrence insectivores. The conservation of these bird assemblages in highly transformed habitats might be compromised (Thiollay 2006).

4.4.2. Local scale

Bird species richness and abundance increased with an increase in invasive alien plant (IAP) cover. Andrén (1994) also showed that due to the expansion of human land use, natural areas become fragmented and reduced in size with generalist species that can make use of small patches, utilising resources in the surrounding environment. Generalists have the ability to use less suitable habitats (Andrén 1994) and could be the bulk of bird species contributing to the increase in bird species richness at local scale.

Agriculture was the most significant determinant of bird species richness at the local scale whilst IAP cover was strongly positively related to bird abundance. Teillard *et al.* (2015) illustrate that agricultural activities result in the displacement of specialist species and gains in generalists such as granivores. Agriculture also leads to an increase in insects which are pests in cultivated areas and subsequently an increase in insect feeding birds (Thiollay 2006). In this study agricultural activities mainly consist of wheat and canola cultivation,

viticulture and sheep and cattle grazing (Rouget 2003). Wheat and canola cultivation as well as pastoralism translates to an increase in food resources for granivores and insectivores. A rise in bird abundance whilst IAP cover increases shows that invaded sites at a small scale can provide appropriate resources for bird sustenance. Johnson (2007) notes that bird abundance is an important measure showing the ability of a habitat to provide conditions such as absence of disease, availability of nesting and accessibility to food resources which are important for the persistence of individuals over a long period. The generalist species that are able to adapt and exploit invaded environments are able to persist in large numbers, although this does not compensate for lost species.

At a local scale, IAP cover positively affected raptors, insectivores and granivores, however, these trends are mainly determined by agricultural activities in invaded areas. The CFR is a predominantly dry environment and agriculture in this area has improved water supply to wildlife, including birds (Okes *et al.* 2008). The large number of artificial watering points creates micro habitats that are important for birds (Okes *et al.* 2008). The direct result of wheat farming and livestock rearing in the CFR is an increase in food resources for all three these feeding guilds and an increase in nesting and perching sites for raptors.

Nectar feeder species richness initially increases in the face of invasion, probably due to the presence of both native and alien nectar producing plants (Le Roux *et al.* 2010; Geerts & Pauw 2013). At this scale, although not clearly showing due to the small sample size (Fig. 4. 6b), a further increase in invasive alien plant cover leads to a decline in species richness as habitat transformation ceases to benefit bird assemblages.

4.4.3 Conclusion

At the landscape scale, trends in bird assemblages in response to IAP cover show evidence for the IDH with diversity being highest at intermediate levels. Patterns in bird assemblages, although also affected by IAP cover, are largely determined by farming and urbanisation at the landscape scale. Different responses to IAP cover at different scales of disturbance eliminate blanket conclusions regarding the effect of invasive alien plants on bird assemblages. A further study into individual species can shed more light on species experiencing range expansions and those facing the threat of extinction due to habitat contraction from invasion by alien plants (Okes *et al.* 2008).

4.5. References

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CHAPTER FIVE GENERAL CONCLUSION AND RECOMMENDATIONS

The presence of invasive alien plants has altered natural systems by displacing native plant species and changing ecosystem structure and functions with impacts on biodiversity conservation (Hood & Naiman 2000; Hobbs *et al.* 2006; Schwartz *et al.* 2006). In South Africa, this need for conservation has driven the government, through the Working for Water (WfW) programme, to participate in initiatives to restore modified ecosystems (van Wilgen *et al.* 1998; 2012; Esler *et al.* 2008). In order to ensure continuation of funding for future clearing projects, WfW needs to show that apart from social aspects, ecological benefits through biodiversity conservation exist (Morris *et al.* 2008). Motivation for restoration is well established and backed up by scientific evidence from a plants perspective, showing conservation gains from clearing. However, studies on faunal responses to plant invasion and post clearing recovery are scarce (Samways *et al.* 1996). Thus the objectives of this study were to assess the response of plants and bird assemblages to invasion and clearing of an alien tree (*Eucalyptus camaldulensis*) at the plot level and to understand if the response of bird assemblages replicates at broader landscape scales.

At the plot scale (chapter 2), the presence of *Eucalyptus camaldulensis* in a riparian system resulted in the significant reduction of bird species richness and abundance with assemblages in invaded sites being almost a complete subset of assemblages in uninvaded sites. I show that the decline in bird species richness and abundance in invaded stands was a result of decreased frugivore and raptor numbers and a complete lack of nectar feeders. I argue that such responses by bird assemblages to invasion have serious consequences to important ecosystem processes such as seed dispersal and bird-pollination. I also show that the drop in raptor numbers due to invasion dilutes the popular notion that eucalypts are important for raptor species for use in roosting, nesting and to serve as hunting platforms. This study adds on to the body of literature highlighting the loss of certain bird feeding guilds and important ecosystem services they provide and motivates for conservation action to preserve wildlife habitat. To ensure the conservation of bird assemblages and important mutualistic services, I recommend, from a birds' viewpoint that invasive alien plant clearing from riparian areas continue.

In chapter 3, the results from the chronosequence assessment of cleared sites of different ages revealed that plant and bird assemblages did not fully recover to near-pristine levels, even a decade after clearing. Plant species composition, vegetation structure and surrounding land use were important in predicting bird assemblages. Although the species richness of native plant growth forms increased following clearing, there is a slow recovery of shrubs and tree species which potentially slowed down bird community recovery. Consistent

with other studies from the same system (Ruwanza *et al.* 2013a, b; Tererai *et al.* 2013), I found an increase in the species richness of alien herbs and graminoids. The presence of alien herbs and graminoids has been cited as a reason for slow native plant recovery, which compromises ecosystem resilience and poses the threat of secondary invasions (Galatowitsch & Richardson 2005; Ruwanza *et al.* 2013a, b). However, bird assemblages responded positively to increases in plant diversity. Most of the displaced bird species including nectar feeders returned to cleared sites. Only raptors showed a slow recovery and I attribute this to the slow recovery of native tree species in cleared sites. I put forward that focused active reintroduction of selected native riparian plants could significantly improve the restoration process for birds at a relatively low cost.

A comparison of my results with other studies from non-riparian habitats in the region (chapter 2) provides a larger picture of the effects of invasive alien plants on bird assemblages in the Cape Floristic Region. I broaden my study from chapter 2 and in chapter 4 I consider the response of bird assemblages to alien plant invasion at larger spatial scales. Results at the landscape scale show evidence for the intermediate disturbance hypothesis (IDH) (Connell 1978) with higher bird diversity occurring at moderate invasive alien plant (IAP) cover. Although I assessed impacts of different levels of invasion at the landscape scale, these results are somewhat similar to patterns shown at the plot scale in chapter 2 where I looked at two extremes of invasion (invaded and near-pristine). At the plot scale, higher bird diversity occurs in near-pristine sites whilst very high IAP cover led to the decline in bird assemblages. In contrast, bird assemblages at the local scale, except for nectar feeders, increased as IAP cover increased. Thus, although driven by different land uses at the local and landscape scales, nectarivores are consistently negatively affected by invasive alien cover regardless of the spatial scale. The rest of the guilds display variable responses to invasive alien plant cover at different scales, which is largely driven by land use.

In summary my study shows that nectar feeders are the most sensitive group of birds to IAP invasions in the CFR and that these obligate mutualists are displaced due to alien plant invasions. Failure to implement restoration activities in order to reclaim and conserve bird habitat and boost nectarivore species richness and abundance, will have far-reaching impacts on plant reproduction. Moreover, results indicate the need for the continuation of clearing for the benefit of negatively affected bird species (e.g. nectarivores) in riparian and terrestrial systems. Although passive restoration based on plant succession brings back some native plants lost to invasion, active re-introduction of selected plant species could accelerate restoration to benefit nectarivores and frugivores.

In order to meet the ultimate restoration goal of a resilient and functional ecosystem, restoration should shift its focus away from evaluating restored sites using vegetative elements only and include animal communities as bio-indicators to assess restoration success (Atkinson *et al.* 2015; Galimberti *et al.* 2016). Assessment of bird assemblages for instance, will point out a list of missing and/or under-represented plant guilds which can be actively reintroduced. Active restoration is an expensive exercise and due to financial constraints, active plant reintroductions should focus mainly on locally available keystone species that are easy to grow. These plant species will assist in the restoration of ecosystem services and functions and which will attract displaced fauna.

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