Cape Peninsula
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A DETERMINATION OF CAPE FLATS SAND FYNBOS RESTORATION SUCCESS IN THE WESTERN CAPE, SOUTH AFRICA, BASED ON VEGETATION ESTABLISHMENT AND POLLINATOR ACTIVITY

by

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DECLARATION

I, Landi Retief, declare that the contents of this dissertation/thesis represent my own unaided work, and that the dissertation/thesis has not previously been submitted for academic examination towards any qualification. Furthermore, it represents my own opinions and not necessarily those of the Cape Peninsula University of Technology.

	31 March 2022
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ABSTRACT

Invasive plant species as well as altered land-use often lead to the degradation of natural areas by displacing native species or by disturbing ecological processes. The consequent restoration of these degraded areas is often associated with high costs. Pollinator visitation can ensure the long-term success of vegetation restoration by facilitating successful plant reproduction and allowing for genetic variability. A diversity of pollinators can also increase stability and colonization rates of newly established plant communities.

The Fynbos vegetation of the Cape Floristic Region (CFR) in South Africa is dominated by small-leaved, ever-green shrubs. The region is characterised by a Mediterranean climate and is highly diverse with a high level of endemism. My study area, Milnerton Racecourse, is a small urban nature reserve (22ha) that consists of critically endangered, Cape Flats Sand Fynbos, a vegetation type that is dependent on fire, but has been severely fragmented in the area where Cape Town is today. Determining the synergistic effect of vegetation restoration treatments, with and without fire, and alternative methods requiring minimal labour (such as topsoil translocation), could assist to identify the most successful and cost-effective treatments to restore native plant communities. Few studies have included pollination as an ecological function to be evaluated as part of active vegetation restoration programmes, even though the long-term survival of plant species is dependent on it. To determine the most successful active restoration methods as well as to understand the effect that the restoration of degraded areas have on pollination, I had two primary aims for the study. Firstly, to determine the success and cost-effectiveness of several vegetation restoration treatment combinations; and secondly, to determine if active vegetation restoration also restores pollination as an ecosystem function.

Over a period of two years, I have tested how successful and cost-effective six combinations of vegetation restoration treatments were. Treatments used were Soil-plant, Soil-mulch-sow-plant, Remove-grass-sow-plant, Burn, Burn-sow, and Burn-sow-plant. Topsoil and mulch were sourced and translocated from an intact natural site. Mechanical methods were used for grass removal. Soil-plant, Soil-mulch-sow-plant and Burn-sow-plant led to plant richness resembling near-pristine plots at 30% higher than Burn. Native shrub cover was the highest for treatments which included planting. Survival for species planted was 36 - 41% higher for Burn-sow-plant. Overall, the contribution of sowing was low, with only 9 - 16% of species sowed, being present across all treatments. Topsoil translocation from a near pristine area can be successful, if combined with planting. Other than topsoil translocation, Burn-sow-plant was the most successful treatment at a reasonable cost, despite the addition of planting, which is less frequently used and expensive, while Burn and Burn-sow were less successful, but cheaper. Remove-grass-sow-plant was the least successful and most expensive treatment. In terms of

pollination, I compared the recently restored and fragmented site with two reference sites (fragmented and intact). I aimed to determine whether pollination was restored by comparing visitation frequency and species richness of pollinators as well as the seed set of seven plant species. The specialization of the tested plant species was also determined, based on the observed pollinator species. Generalist plant species all produced seed set equivalent to that produced from optimal pollination, whether they were capable of autonomous selfing or not. Specialist plants that were incapable of autonomous selfing were absent from fragmented study sites and even when introduced at these sites, pollination was low or non-existent. While species richness (45-100%) and visitation frequency of pollinators visiting the generalist species *Moraea flaccida* and *Ornithogalum thyrsoides* were both higher at the intact site, natural seed set for the species indicated optimal pollination at all sites. *Ferraria crispa*, a generalist plant species primarily pollinated by Dipterans, had a higher species richness and visitation frequency of pollinators at the restored site (55%) and the fragmented reference site (55%).

I identified several factors in addition to fragmentation and vegetation restoration that can affect pollination in natural sites that seem to be complex and different for individual plant species. These factors included surrounding land-use, distance to the urban edge and specialization. My results show that generalist plant species have a greater potential to facilitate ecosystem recovery in terms of pollination. Providing sustained nectar sources, high floral abundance and stepping-stones for specialist pollinators, such as sunbirds in South African Fynbos, might aid their movement to restored habitat fragments. This study shows that a combined approach of vegetation restoration ecology and pollination biology, with a plant species-specific approach to accommodate pollinator species should be used when planning active restoration.

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GLOSSARY

Acronyms/Abbreviations

AIC	Akaike's Information Criterion
ANOVA	Analysis of variance
CCT	City of Cape Town
CFR	Cape Floristic Region
CFSF	Cape flats sand fynbos
emmeans	Estimated Marginal Means
GLM	Generalized linear model
GLMMs	Generalized linear mixed models
ha	Hectare
HSD	Honest Significant Difference
kg	Kilogram
km	Kilometre
km^2	Square kilometres
m	Metre
m^2	Square metres
mm	Millimetres
MuMIn	Multi-Model Inference
UN	United Nations
USD	United States Dollar
ZAR	South African Rand

CHAPTER ONE
GENERAL INTRODUCTION

1.1 Introduction

As we move into the United Nations' Decade on Ecosystem Restoration, the ecosystem approach of the Convention on Biological Diversity is becoming increasingly important as we strive to restore degraded landscapes and their ecosystem function. Martin (2017) describes ecological restoration as the recovery of ecosystem conditions that maintains ecological structure, process and function. Furthermore, ecological restoration is the process of assisting the recovery of an ecosystem that has been damaged, degraded or destroyed (Gann et al., 2019). While restoration usually entails the re-establishment of native vegetation on a site, ecological restoration also aims to restore process linkages to restore a system that is sustainable in the long-term (Ehrenfeld & Toth, 1997). These process linkages include pollination, which is essential for the long-term survival of vegetation and can ensure the sustainability and functionality of restored systems (Kollmann et al., 2016).

Pollinators could be absent at restored sites due to limited food sources in small scale restoration projects, lack of nesting sites and increased predation (Donaldson et al., 2002; Harrison & Winfree, 2015). However, pollinators may not even be able to disperse to fragmented restoration sites due to a lack of connectivity (Johnson, 2004). Due to global large-scale fragmentation and habitats being disturbed, non-flying or restricted-range pollinators may be completely excluded from new areas, especially when no natural corridors are present (Holmes, 2000; Menz et al., 2011; Sánchez-Bayo & Wyckhuys, 2019). Smaller areas are also less likely to support pollinators and seed dispersers. Consequently, this may lead to a loss of viability of plant populations due to a reduction in cross-pollination and natural selection (Holmes & Boucher, 2001). Connectivity leads to a greater robustness against secondary extinctions following disturbances (Forup et al., 2008), therefore it is imperative to also have pollination available as a function to increase the reproduction of plant species and the consequent success of a vegetation restoration project.

1.2 Vegetation restoration

Vegetation restoration techniques can be divided into active and passive restoration (Atkinson & Bonser, 2020). Active restoration usually includes interventions that aim to facilitate recovery (Holl & Aide, 2011); passive restoration is when no management actions are taken, except for removing the causes of environmental disturbances (Morrison & Lindell, 2011). In complex situations where passive restoration does not lead to the desired outcomes, active restoration must be applied by reintroducing native species to the area (Holmes et al., 2020). Research has shown that passive restoration is mostly unsuccessful, in particular if restoration sites

have been drastically altered by long-term disturbance and if resilience has been reduced (Le Maitre et al., 2011; Gaertner et al., 2012). This is particularly important for threatened vegetation types in urbanized areas, such as lowland Fynbos in South Africa, of which the largest extent is located within Cape Town, one of the fastest growing cities in the world (Rebelo et al., 2011).

The Fynbos biome in South Africa is located within the Cape Floristic Region (CFR) and is the smallest of the six plant kingdoms in the world and the only one limited to one country (Blokker et al., 2015). Small-leaved, ever-green shrubs dominate the vegetation of the biome (Rebelo et al., 2006). The CFR is characterized by approximately 9 000 species of flowering plants, occupying an area of 90 000 km^2. Two thirds of these species are endemic to South Africa, and almost 2000 species are rare or endangered (Raimondo et al., 2009). The survival of Fynbos is strongly dominated by and dependent on fire (van Wilgen, 2009).

Cape Flats Sand Fynbos (CFSF) is a critically endangered lowland vegetation type found within the CFR (Skowno et al., 2019). CFSF is endemic to Cape Town, a city hosting more than 80% of the 5.8 million people living in the Western Cape of South Africa (Helme et al., 2016). More than 85% of the original extent of the vegetation type has been destroyed (Rebelo et al., 2006). Because of this, the conservation target of 30% for CFSF remains unattainable (Holmes & Pugnalin, 2016). Most remaining patches of CFSF are surrounded by urban areas. Some of these areas are actively managed by conservation authorities. Those that are not, are subjected to threats such as urban development and invasive alien plants (Mostert et al., 2017). Even though there has recently been an increase in research on restoration of CFSF, there is a need to monitor the success of restoration in terms of vegetation recovery (Krupek et al., 2016; Hall et al., 2021) and of ecosystem services such as pollination (Holmes et al., 2020).

1.3 The cost of restoration

With limited resources available for restoration (Krupek et al., 2016; Blignaut & Aronson, 2020) it has been recommended that the focus be shifted to less degraded sites where passive restoration will be more successful (Holmes et al., 2020). However, CFSF, the most transformed of all Fynbos vegetation types, is known to have a low potential to spontaneously restore (Holmes et al., 2020). This necessitates active restoration, which pose challenges in terms of the success of restoration methods and their cost. Invasive alien plants have been described as the second biggest threat – after urbanization – to conservation in Cape Town (Rebelo et al., 2011). The removal of invasive alien plants usually prelude restoration to remove disturbance, but is expensive (Marais et al., 2004; McConnachie et al., 2012), which further exacerbates the already high costs of restoration projects. Other challenges that may

be encountered are that active seed application and the resultant seedlings in Fynbos restoration projects can attract granivores and herbivores (Iponga et al., 2005) whereas erecting fences or exclusion plots are often costly. Seeds may also fail to germinate due to dormancy (Florentine et al., 2011) or them being buried too deep (Christian & Stanton, 2004), while propagating plants for restoration projects is often costly (Holmes, 2008; Greet et al., 2020) and labour-intensive (Ruwanza et al., 2013).

It is imperative to optimize restoration outcomes by using the most successful treatments at the lowest cost (Kimball et al., 2015). As we enter the UN's Decade on Ecosystem Restoration, cost-effectiveness will become even more important as the emphasis is on scaling up restoration projects (Suding et al., 2015, http://www.bonnchallenge.org/, https://www.decadeonrestoration.org/), while funds remain limited. Despite this, the costs of restoration treatments are rarely reported and even less so analyzed (Holl & Howarth, 2000). In fact, in a recent review (Acosta et al., 2018) it was found that only 11% of restoration publications analysed the cost-effectiveness of treatments.

1.4 Pollination and restoration

Approximately 90% of flowering plants rely on pollinators for reproduction, while pollinators themselves obtain food from flowers (Kaiser-Bunbury et al., 2009; Ollerton et al., 2011). Ecologically specialized plant species will attract only a particular group of pollinators, while generalized plant species will use a broader spectrum (Johnson & Steiner, 2000). According to Stebbins (1970), plants should specialize on fewer pollinators when pollinator availability is reliable, whereas generalist pollinators should utilize plants when pollinator availability is unpredictable. Annual plants that are short-lived and can only reproduce by seed are normally expected to be generalists (Waser et al., 1996). Conversely, specialist plants are normally long-lived plants, with pollinators that show a high degree of fidelity to a single or small number of specialist plant species to ensure pollination (Bond, 1994). In biodiversity hotspots, such as the CFR which is plant-species rich, plants are more likely to have high levels of pollinator specialization due to the increased competition for pollinator services (Dixon, 2009; Johnson, 2010; Geerts et al., 2020). However, the specialist pollinators on which specialist plants are dependent, can become more vulnerable to local extinction when resources start to decline (Pauw, 2007).

A reduction in pollinators can lead to negative consequences such as lowered seed set or increased inbreeding (Geerts, 2016; Sabatino et al., 2021). Consequently, pollination plays an important role in ensuring the sustainability of restored ecosystems (Potts et al., 2010) and is one of several ecosystem functions that must be reinstated for restoration to be successful (Forup et al., 2008). While the conservation of all biodiversity is important, restoration attempts

should consider pollinators due to the benefits they hold for plant reproduction and genetic resilience (Dixon, 2009; Menz et al., 2011; Kollmann et al., 2016). Concerns about a global decline in pollinators have increased investigation on habitats that can support them (Hopwood, 2008). Ultimately, the survival of plant species depends on the presence of the necessary pollinators and seed dispersers being present (Ollerton et al., 2011; Hernández-Villa et al., 2020). Yet globally (Menz et al., 2011) and in Africa (Rodger et al., 2004; Genes & Dirzo, 2022), relatively few studies have focused on plant-pollinator relationships in the restoration of non-agricultural systems (but see Forup & Memmott, 2005; Forup et al., 2008; Kaiser-Bunbury et al., 2017; Ritchie et al., 2020; Mnisi et al., 2021).

1.5 Restoring for functional ecosystems

Due to the wide variety of conditions within degraded sites globally, the choice of restoration treatments used are site-specific (Falk, 2006; Hall et al., 2021). As an example, the success of topsoil transfer as a stand-alone restoration treatment, largely depends on whether a native seedbank is present (Fowler et al., 2015; Golos et al., 2016). Given that the treatment may vary from site to site (GeFellers et al., 2020), this will influence the success of the outcome. The significant effects of fire on fire-adapted systems have not only been studied globally (Bond & Keeley, 2005), but also in South Africa within the Fynbos biome (van Wilgen, 2013). This has also been coupled with sowing (Holmes, 2008; Pretorius et al., 2008; Gaertner et al., 2012; Ruwanza et al., 2013; Kraaij et al., 2017) and studies on the germination requirements of seeds (Brown et al., 2004; Hall et al., 2017; Mukundamago et al., 2017). Due to the extensive problem of *Acacia saligna* as an invader within the Fynbos biome (Krupek et al., 2016), there has been limited attention on restoration in unburnt areas through mechanical or chemically removing invasive grass layers (Holmes, 2008). This despite alien grasses being a major problem as invaders or secondary invaders after the removal of invasive alien trees (Gaertner et al., 2012). Most of the work done in the CFR is focused in areas either invaded by or recently cleared of *Acacia saligna* (Holmes, 2008; Pretorius et al., 2008; Gaertner et al., 2012; Ruwanza et al., 2013; Fill et al., 2017) as this species is one of the main threats to Fynbos - especially in the lowlands (Rebelo et al., 2006). Due to the drastic and long-lasting effects of *A. saligna* on the soil characteristics of restoration sites (Yelenik et al., 2004; Nsikani et al., 2018) the restoration of degraded old fields without previous invasion of the species does require a different site-specific approach (Gaertner et al., 2011; Holmes et al., 2020). The combined use of seed and planting could be very successful in these areas, but have received limited attention, primarily due to the perceived higher costs of using propagated plants (Holmes, 2008; Greet et al., 2020). Restoration success is usually assessed by whether the structurally representative plant communities of vegetation and native plant diversity have been restored (SER, 2004). However, recently there has been a change in emphasis in the

restoration field, with the restoration of ecological functions receiving more attention (Menz et al., 2011; Devoto et al., 2012; Kollmann et al., 2016). This leads to restoration initiatives adopting a functional rather than just a structural approach (Suding et al., 2015; Martin, 2017).

Restoration projects therefore differ in their goals, as some may have the objective to reintroduce native species while others may aim to reintroduce ecosystem functions such as pollination (Majer, 2009). In a review where 224 recent ecological restoration publications were considered, it was found that 42% of studies did not consider ecosystem function and of those that did, there were only two terrestrial studies from Africa (Kollmann et al., 2016). While restoration studies should include the monitoring of animal groups such as pollinators, which are drivers of ecosystem processes (Dixon, 2009), there is still a general paucity of the integration of pollination and vegetation restoration, especially within the African context.

Pollination is an important ecosystem function as many plants rely on it for reproduction (Ollerton et al., 2011) and to maintain genetic variability (Menz et al., 2011). However, only 0.03% out of 355 reviewed African publications on pollination biology considered the conservation application of this field, even though indigenous plants need these pollination systems to be effectively conserved (Rodger et al., 2004). Over time, the situation has largely remained the same, as during a review in 2018 it was found that globally only 2.9% of 419 restoration publications included invertebrates within the study (Acosta et al., 2018). The number of pollination studies in the CFR proves to be disproportionately high, when compared to the rest of Africa, although globally the majority of pollination studies done are of an evolutionary nature (Rodger et al., 2004). The inclusion of pollination within restoration studies is specifically important in the light of a global decline in pollinators (Hopwood, 2008) and the increasing environmental threats posed to pollination as a vital ecosystem function (Bascompte & Jordano, 2007; Ollerton et al., 2011; LaBar et al., 2014; Ramos-Jiliberto et al., 2020).

Habitat fragmentation globally poses a major threat to biodiversity (Sandberg et al., 2016). A common threat in fragmented areas is that small populations will not be able to survive adverse environmental conditions if the number of individuals per species is below a certain threshold (Helme et al., 2016). Furthermore, the degree of recovery of a restoration site may depend on the proximity to source populations in the surrounding landscapes (Forup et al., 2008). Therefore small, isolated remnants of less than 100 ha are more at risk to losing species due to altered ecological processes and environmental fluctuations (Helme et al., 2016). Invasive alien plants often contribute to altering ecological processes and accelerates the degradation of areas by displacing native plant communities (Holmes et al., 2020). While pollinators are critical for restoring native plant communities (Kaiser-Bunbury et al., 2017),

some species may be negatively impacted by factors such as fragmentation and habitat loss (Winfree et al., 2011) due to the greater difficulty of dispersal as well as reduced floral resources within smaller areas (Potts et al., 2010). Invasive alien plants may also disrupt the pollination of native plant species by decreasing the amount of available native floral resources or by influencing the foraging behaviour of insect pollinators (Ghazoul, 2004; Cariveau et al., 2020). The negative effects of invasive alien plant species on invertebrate pollinators (Greenwood et al., 2004; Gerber et al., 2008) can eventually cascade to the bird pollinator groups in an area (Proches et al., 2008; Simberloff et al., 2010; Holland-Clift et al., 2011; Mangachena & Geerts, 2017; Adedoja et al., 2021).

Fairly recently, restoration ecologists have started to broaden restoration studies to also include ecosystem functions, such as the dispersal and migration of pollinators to restored sites (Cariveau et al., 2020). The success of restoration projects in CFSF is usually interpreted by only looking at the structural aspects of the restored vegetation (but see Mnisi et al., 2021), while the assessment of the subsequent return of pollinators to restored sites in this endangered vegetation type have been largely overlooked (Genes & Dirzo, 2022). This, despite the fact that the survival and reproduction of restored plant species may be dependent on pollination as an ecological function (Ollerton et al., 2011). Due to the small remaining extent of CFSF and the fact that remnants are highly fragmented (Holmes & Pugnalin, 2016), the natural migration and dispersion of insect and bird pollinators to these areas may be hampered (Pauw, 2007). However, using restoration techniques such as prescribed burning, sowing and planting in combination with each other to ensure a high native plant diversity, might allow for pollination as an ecosystem function to be restored.

1.6 The research problem

Ruiz-Jaen & Aide (2005) found that of 468 publications, only 15% evaluated the success of restoration projects afterwards, with 53% of those studies being conducted in North America and only 4% in Africa. To determine the success of restoration studies, it is critical to have one or more reference sites to be able to measure the degree of restoration achieved (Gann et al., 2019). In a review by Wortley et al., (2013) it was found that of 301 restoration publications, more than 50% of studies did not use reference sites - despite the necessity thereof (Ruiz-Jaen & Aide, 2005). Since restoration outcomes are often unpredictable, testing the effectiveness of restoration treatments improves the chance of outcomes to meet restoration objectives, while also ensuring cost-effectiveness (Brudvig & Catano, 2021). With funding and resources in South Africa usually being limited (Holmes et al., 2020), research on the cost-effectiveness of restoration treatments in a fragmented and critically endangered habitat such

as CFSF is needed. Even more so, the cost of restoring of old fields within areas of lowland Fynbos in the absence of woody invasive alien plant species (Holmes, 2008) has been largely overlooked.

However, the value of restoring plant species if their pollinators cannot be restored, is limited at best (Forup & Memmott, 2005). Pollinators are important in ecosystem functioning and are declining globally (Losey & Vaughan, 2006). This reduction can drastically reduce plant reproduction and gene flow (Hopwood, 2008). Research indicates that the difference in plant species composition strongly affected which pollinator communities were interacting with plant species (Kaiser-Bunbury et al., 2017). Restoration projects should therefore prioritize for restoration sites to not only support diverse plant communities, but also pollinator assemblages to ensure the long-term survival of plant species (Kaiser-Bunbury et al., 2009).

In this thesis I determine the success and cost-effectiveness of restoration efforts – not only by investigating the structural aspects of vegetation restored by different restoration treatments – but also by quantifying the visitation of pollinators on key plant species. When these aspects are compared between a restoration site and intact, functional natural sites, it might allow insight into the success of also reinstating key species linkages (Ehrenfeld & Toth, 1997).

1.7 Thesis outline

This thesis consists of four chapters of which two are data chapters. Chapter one is a general literature review on the main concepts of the study, including research problems and aims. In addition, it provides a detailed overview of chapters to be included in this thesis. Chapter two assesses the success of various restoration treatments in terms of vegetation recovery and cost-effectiveness. The focus in chapter three is on determining whether an active plant focused restoration approach restores pollinator visitation to flowering plants. Chapter four concludes and consolidates the study.

1.8 Aims

The aim of this thesis was to consider the synergistic effect of different combinations of restoration treatments (i.e. fire, seed, planting, topsoil translocation, mulch and the mechanical removal of invasive grass layers) and to consequently weigh up the success and cost of these treatments in order to identify the most cost-effective options for restoration in CFSF. Secondly, pollination as an ecosystem function was assessed, to determine the effect of active vegetation restoration and fragmentation on pollination. Specifically, I aimed to determine:

- Can the use of fire and topsoil translocation successfully restore native plant communities if used in combination with additional restoration treatments such as sowing and planting?

- Which combination of restoration treatments are the most cost-effective to use in Mediterranean systems such as Fynbos?

- Does an active plant-focused restoration approach restore pollinator visitation, pollinator species richness and subsequent seed set of generalist and specialist plant species?

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CHAPTER TWO

ECOLOGICAL RESTORATION AFTER PRESCRIBED BURNING AND TOPSOIL TRANSLOCATION: ASSESSING THE SUCCESS AND COST-EFFECTIVENESS OF VARIOUS RESTORATION TREATMENTS IN SOUTH AFRICAN FYNBOS*

2.1 Abstract

The successful restoration of endangered habitat types at a low cost is of vital importance as we enter the United Nations Decade of Ecosystem Restoration. Over a period of two years, we have tested how successful and cost-effective six combinations of restoration treatments were in the Cape Floristic Region of South Africa. Treatments were applied to an area that was formerly used for horse training and primarily covered in invasive alien grasses. Treatments used were Soil-plant, Soil-mulch-sow-plant, Remove-grass-sow-plant, Burn, Burn-sow, and Burn-sow-plant. Topsoil and mulch were sourced and translocated from an intact natural site. Mechanical methods were used for grass removal. Soil-plant, Soil-mulch-sow-plant and Burn-sow-plant led to plant richness resembling near-pristine plots and ~30% higher than Burn. Native shrub cover was the highest for treatments which included planting. Survival for planted species was 36–41% higher for Burn-sow-plant than for other treatments. Overall, the contribution of sowing was low, with only 9–16% of species sowed being present across all treatments. We show that topsoil translocation can be successful – in the rare case of translocation from a near pristine area – if combined with planting. Other than topsoil translocation, Burn-sow-plant was the most successful treatment at a reasonable cost, despite planting being expensive, while Burn and Burn-sow were less successful, but cheaper. Remove-grass-sow-plant was the least successful and most expensive treatment. We conclude that the most successful treatments are not necessarily the most expensive.[1]

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* Note that Chapter 2 is currently under review in the journal Restoration Ecology. This paper has more than one author - hence the use of the word 'we'. The student (L. Retief) is the first author and designed the study, did the data collection, data analysis and manuscript writing, while the supervisors helped with conceptualising ideas, planning, statistical analysis and commented on manuscript drafts.

2.2 Introduction

Invasive alien plants can alter ecosystems processes and reduce the abundance of native plant species (Levine et al., 2003). Without intervention, invasive alien plants will continue to dominate a landscape, outcompeting native plant species and in the process hindering the restoration of native plant communities (Joubert, 2009). Management interventions to remove invasive alien plants are often costly and labour-intensive (Gaertner et al., 2012), and passive restoration after clearing is often not sufficient to facilitate full recovery (Suding, 2011). Re-invasion (Holmes et al., 2020), secondary invasion (Nsikani et al., 2020), soil legacy effects of invaders (Nsikani et al., 2018), and/or depleted native seed banks (Holmes & Richardson, 1999) can hinder successful restoration outcomes. In fire-driven ecosystems such as Mediterranean systems, prescribed burning after alien clearing can stimulate the germination of soil stored native seedbanks (Vlok & Yeaton, 1999; Montenegro et al., 2004; Keeley, 2012; Esler et al., 2014). Fire is a cost-effective treatment for the restoration of Mediterranean systems and far less labour-intensive than other methods (Jackson et al., 1982; Musil et al., 2005). Native seed forms an important component of restoration projects (Nevill et al., 2018) because it can facilitate and accelerate the recovery of vegetation (Palma & Laurance, 2015). However, when soil seed banks are small, relying on sowing can pose a challenge as seed harvesting is time-consuming (Broadhurst et al., 2016), whilst commercial native seed stock is not always available and can be costly (Cross et al., 2020).

Perennial shrub species in Mediterranean systems may not survive well as seed (Holmes, 2008), because most plant species growing from seed banks have been found to be annuals and short-lived forbs and shrubs (Holmes & Richardson, 1999). Therefore, it is beneficial to also plant propagated plants after a prescribed burn (Hall et al., 2021). However, the planting of propagated plants in burnt areas is uncommon in South Africa (but see Midoko-Iponga et al., 2005; Ruwanza et al., 2013), while globally, there is an insufficient number of studies to conclusively show benefits of these methods (Palma & Laurance, 2015; Nolan et al., 2021). Using sowing in combination with planting has recently been recommended as a combination treatment to achieve better restoration outcomes (Greet et al., 2020; Hall et al., 2021). The advantage of using seed in combination with plants is that the latter provides better cover for the former to germinate and to survive (Godefroid et al., 2011). For many species germination percentage is often low due to germination requirements – such as specific microclimates – being absent (Hall et al., 2016). The planting of propagated plants as nurse plants can thus increase restoration success (Holmes & Richardson, 1999) by helping to create the microclimates that are favourable for the germination of seeds and survival of seedlings (Ruwanza, 2017). However, propagation of plants can be costly (Ruwanza et al., 2013), especially for large areas (Rodrigues et al., 2009). This highlights the trade-off between

success versus cost, as propagated plants often survive better (Cole et al., 2011) - which increases restoration success but, in turn, costs more. Determining the synergistic effect of fire in combination with sowing and planting could potentially assist to identify the most cost-effective combination of treatments.

Globally, the use of topsoil translocation for ecological restoration has increased in recent years, with the majority of studies focused on post-mining areas (Fowler et al., 2015). Few studies have used this in Mediterranean systems other than south-eastern France (Bulot et al., 2014; Jaunatre et al., 2014; Bulot et al., 2017; Buisson et al., 2018; but see Holmes, 2001; Ruwanza, 2020). Topsoil that is translocated from intact donor sites to degraded areas not only aids in translocating seeds, but also potentially translocate other plant propagules and microorganisms (Buisson et al., 2018) that are essential for germination and growth. Topsoil translocation has been shown to be successful if combined with other methods such as planting, although the woody shrub component of vegetation remains difficult to restore with this method (Pilon et al., 2019). Furthermore, the outcome of topsoil translocation is largely dependent on a rapid operation, with minimal or no stockpiling (Koch, 2007), at the right time of the year (usually autumn for Mediterranean areas) (Bulot et al., 2014), as well as translocating topsoil to an area the same size as the donor site (1:1) (Buisson et al., 2018). However, the method does pose a risk of introducing invasive alien species to newly restored sites, by transporting seed within the translocated soil, which could potentially compromise donor sites (Ferreira et al., 2015). The application of mulch to restoration areas is known to improve soil characteristics (Zribi et al., 2015) and seedling establishment (Benigno et al., 2013). The question whether the effect of mulch – after soil translocation – enhances seed germination and seedling establishment, has received limited attention in Mediterranean systems (but see Holmes, 2001; Tormo et al., 2007; Benigno et al., 2013). The high costs associated with harvesting and applying mulch have been found to be unjustified in terms of the little benefit it provided in Australian Banksia woodlands (Rokich et al., 2002) - although, this may be different for other Mediterranean systems.

Cost-effectiveness of different restoration treatments is important, but often ignored (Acosta et al., 2018). Ecological restoration is expensive; therefore, it is imperative that research considers not only restoration treatments that are potentially most successful, but also those that are most cost-effective. Even more so, research should provide guidance on the interaction between success and costs. Success can be measured in various ways, but often vegetation structure, species diversity and abundance is used (Wortley et al., 2013). While it is not necessary to reintroduce all species to reinstate ecosystem functions, the higher the plant species richness, the more resilient the ecosystem will be in the long-term (Holmes & Richardson, 1999).

Our study took place within the Fynbos ecosystem of the Cape Floristic Region (CFR) in South Africa. The CFR is characterized by a Mediterranean climate, with winter rainfall and hot, dry summers. Fynbos is an ever-green shrubland of which more than 5% of plant communities usually consist of Restionaceae. Furthermore, Ericaceae and Proteaceae shrubs usually dominate the landscape, with ephemerals and geophytes being mainly present after the occurrence of a fire (Rebelo et al., 2006). The majority of woody shrubs within Fynbos survive as obligate reseeders while the seedbanks of Restionaceae and Proteaceae are mostly long-term persistent (Holmes & Newton, 2004). The survival of Fynbos is strongly influenced by fire (Bond & Van Wilgen, 1996; Van Wilgen et al., 2010; Keeley, 2012; Geerts, 2021)). If a native seed bank no longer exists, restoration attempts should also include the reintroduction of native plant species, either through sowing or planting (Pretorius et al., 2008). Cape Flats Sand Fynbos, a lowland Fynbos type, is prone to disturbance, especially through the invasion of alien annual grasses (Rebelo et al., 2006).

Here, we aim to address some of these questions by considering the synergistic effect of different combinations of restoration treatments (i.e. fire, seed of forbs and annuals, planting of woody shrubs, topsoil translocation, mulch and the removal of invasive grass layers). Specifically, we addressed the following questions: 1) Does the synergy of fire, seed and planting provide greater restoration success than other methods? 2) Can topsoil translocation and subsequent planting lead to full plant community recovery? 3) Does the planting of woody shrubs as an active restoration treatment restore native shrub cover? and 4) Is a prescribed burn more cost-effective than planting native plants and mechanically removing alien grasses?

2.3 Methods

2.3.1 Study area

Our study area was located within Milnerton Racecourse reserve, a small (22 ha) urban nature reserve in the CFR of South Africa (Fig. 2.1). Milnerton Racecourse reserve is one of the last remaining remnants of Cape Flats Sand Fynbos (CFSF), a critically endangered vegetation type found within the CFR (Rebelo et al., 2006).

In 2015, the nature reserve acquired 3 ha of degraded land, adjacent to the existing reserve (Fig. 1; Site 1 & 2). The site was taken over in 2017 by the City of Cape Town, to be restored and managed as a nature reserve. As part of a land exchange agreement, 0.561 ha of well-managed CFSF was lost (Fig. 1; Lost Site), but this topsoil and resultant mulch from vegetation here, was translocated to the degraded area (Fig. 1; Site 2). Control plots within the reference site were selected in the adjacent intact nature reserve, within part of the same vegetation community of the site that was lost. The reference site as well as Lost Site where topsoil and

mulch were sourced from, were in near-pristine condition. Areas which received the Burn, Burn-sow and Burn-sow-plant treatments were previously used as a polo field and had an estimated 20% cover of alien grass species. The Soil-mulch-sow-plant and Soil-plant treatments were applied to an area was previously used for horse-training activities. The area consisted of several parade rings as well as an old road covered with nutrient-rich laterite (Fig. 2.6a & 2.6b). The Remove-grass-sow-plant treatment was applied to the areas next to the horse parade rings. An estimated 60% of this site was covered with alien grass species, with a low abundance of other invasive weed species present. Control measures were put into place to exclude herbivores (*Raphicerus melanotis*, Cape grysbok) from the restoration site. Raptor perches were set up to limit possible granivory. It must be acknowledged that Cape Town experienced a severe drought during the three years prior to restoration treatments taking place with an annual rainfall which was at 20-47% lower than the normal average.
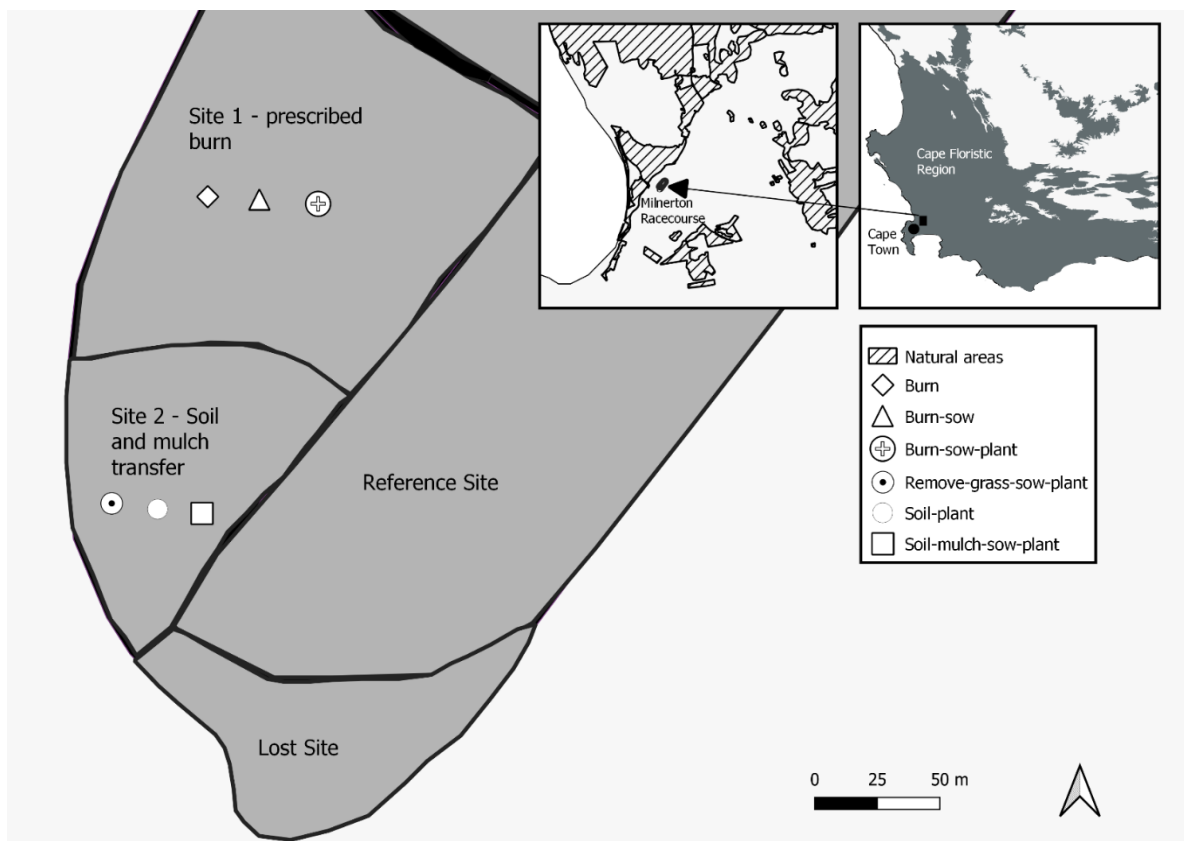
Figure 2.1 The study was located within Milnerton Racecourse, a small urban nature reserve in the Cape Floristic Region (CFR), South Africa. The site was divided into four areas as indicated on the map - the Lost Site, the Reference Site as well as two sites (Site 1 and 2) that each received a number of different restoration treatments. *Right inset* The extent of the CFR as well as the location of Milnerton Racecourse. *Left inset* The remaining natural areas around the study site.

2.3.2 Restoration treatments

2.3.2.1 Topsoil and mulch translocation

The translocation of topsoil from the lost site (Fig. 2.6c) to a part of Site 2 (Fig. 2.1) took place during autumn 2017 before the first winter rains. The lost site received a prescribed burn, 7 years prior to topsoil translocation. The vegetation was cut to ground level with brush cutter machinery and passed through a shredder. The resulting mulch was mixed with topsoil to create a soil-mulch blend. This was immediately spread out on Site 2 with minimal stockpiling taking place. Artificial laterite in Site 2 was removed from a depth of 200-300 mm and replaced with either topsoil or a soil-mulch blend of the same depth from the lost site. Topsoil was translocated at a ratio of 1:1 (Buisson et al. 2018).

2.3.2.2 Prescribed burn

A prescribed burn was done on Site 1 (Fig. 2.1; Fig. 2.6d). This took place during autumn on a mild sunny and windless day. A head-fire was used, together with drip torches and leaf blowers.

2.3.2.3 Reintroduction of plant species

Seeds and cuttings were sourced from the Milnerton Racecourse nature reserve. Seeds were treated with a dry smoke method. Sowing was done by broadcasting and embedding seeds, one day after the prescribed burn. Seeds of annual and perennial forbs, shrubs and geophytes were sown at 10 kg/ha within 24 monitoring plots (Esler et al., 2014). The seeds of 18 different plant species were sown. For propagation, plant material was propagated into a mix of 50% sand from the restoration site and 50% nursery soil. Plants were hardened off within 1-kg bags, in full sun, 2 weeks prior to planting. Planting in the restoration site took place after a cold front that had occurred during winter. Perennial shrubs were planted out at 2,800 plants/ha within 24 monitoring plots. Nine different plant species were planted out. Plants were planted in groups or "islands" of three to four plants to ensure better cover and micro-climates for the germination and survival of seeds (Cowell, 2014).

2.3.2.4 Alien grass removal

The plots used for the Remove-grass-sow-plant treatment (Table 2.1) were primarily covered in alien grass species. Within these plots, the grass layers were removed together with the top layer of soil (10 mm). Removal was done manually with spades and material was removed from the site.

2.3.3 Sampling design and vegetation monitoring

Data was collected once a year, during the months of September and October. Due to the limited area that was available for topsoil and mulch translocation, as well as the limitations of a small urban study site with the risk of edge effects compromising plots, not all restoration treatment factors could be tested separately. Data was collected prior to the restoration treatments taking place, from six single rectangular 50m^2 plots within the area that was lost. Thereafter it was collected for 2 more years after restoration treatments had taken place. During these 2 years, data was collected from 42, single rectangular, 50m^2 plots. Six 50m^2 replicas were used in separate areas for each of the six restoration treatments as well as for a reference site which was approximately 50 meters from the experimental site within the neighbouring nature reserve (Figure 2.1). Year 1 and Year 2's data collection took place respectively, 5 months and 18 months after restoration treatments. Species presence was recorded, and species were classified according to status (native, alien), and growth form (graminoid, forb, shrub). The species presence of plant species that were either sown or planted were recorded

2.3.4 Financial analysis

An analysis of the costs of restoration treatments was done. Costs were calculated in South African Rands/ha (1 ZAR = 0,069 USD; 12 July 2021). All expenses of each restoration factor were calculated, including labour, as well as the resources needed for the preparation and execution of treatments. Where it was cheaper and practical, the hiring costs of items were used. Two quotations were obtained where applicable, from which the average was then calculated. The cost of labour was calculated according to the set minimum wage per day in South Africa (South Africa, 2021). All total costs were scaled to depict the cost of each treatment per 1 ha to 50 ha (Blignaut et al., 2014). The cost of treatments was linked up with the success of treatments in terms of native species richness.

As the cost of many of the resources used for fire as a restoration treatment remains the same even as the amount of hectares increases, this treatment was scaled as follows: 20 crew members with tools were allocated for a 1 ha fire, which was increased with one crew member with tools for every 5 ha added; three fire fighting utility trucks were assigned for a 1 ha fire, which was increased with one fire fighting utility truck for every 10 ha added; and 60 liters of drip torch fuel were assigned to a 1 ha fire, which was increased with 60 liters for every 10 ha added.

2.3.5 Statistical analyses

Statistical analyses were conducted in R version 4.0.3 (R Development Core Team, 2020). Generalized linear mixed models (GLMMs) were fitted using the glmmTMB package (Magnusson et al., 2020) to determine the effect of (1) restoration treatment, years after treatment, and their interaction on native and alien species richness (Poisson error distribution and log link function); (2) restoration treatment, growth form, and their interaction on native species richness (Poisson error distribution and log link function); and (3) restoration treatment, years after treatment, and their interaction on planted and sowed species survival (Beta error distribution and logit link function). "Plot" was included as a random effect to account for variability between plots and to quantify spatial variability. Different models were compared via dredging, an automated procedure implemented by the *MuMIn* package (Barton, 2018), to identify variables that best explain the variability in native and alien species richness. Models were compared using information theoretic model procedures based on Akaike's information criterion (AIC; Burnham et al., 2011). The best-fitting model was chosen using the second order AIC value, AICc. The model with the lowest AICc value was chosen as the best-fitting model as it had the smallest information loss, even if it did not include all the explanatory variables. For each response variable, only one model remained after model selection. Results of these best-fitting models are reported here. Significant mean differences were separated with Tukey's HSD (Honest Significant Difference) test using the *emmeans* package (Lenth, 2018).

Table 2.1. A summary of the factors included in each restoration treatment. Individual treatment components included the translocation of topsoil and mulch, the mechanical removal of an invasive grass layer, the application of fire, the sowing of seed as well as planting.

Site		Burn	Sow	Plant	Soil	Mulch	Remove grass
1	Treatment 1	✓					
	Treatment 2	✓	✓				
	Treatment 3	✓	✓	✓			
2	Treatment 4			✓	✓		
	Treatment 5		✓	✓	✓	✓	
	Treatment 6		✓	✓			✓

2.4 Results

2.4.1 Effects of restoration on vegetation parameters

In an analysis of the effect of restoration treatment, years after treatment and their two-way interaction on native species richness, "year" was not significant in the best fitting model. For Burn-sow-plant (Fig. 2.6e), Soil-mulch-sow-plant, and Soil-plant (Fig. 2.6f), native species richness was similar to the reference site ($p = 0.99$; Fig. 2.2; Table S1). Burn, Burn-sow, and Remove-grass-sow-plant had a significantly lower native species richness than the reference site ($p < 0.01$; Fig. 2.2; Table S1).

There was a significant difference in the alien species richness of treatments between the first and second year ($p < 0.01$; Table S2), as overall there were fewer alien species present in the second year (Table S3). Of all treatments, the lowest number of alien plant species was found within Burn-sow, during the second year (nine species; Table S3). The three restoration treatments that involved the use of fire all had a lower number of alien plant species than treatments that did not involve the use of fire (Table S3).

The treatments that included the use of planting as a restoration factor, all had a significantly higher native shrub cover than those treatments that did not, including the reference site ($p < 0.05$; Fig. 2.3; Table S4). Native forb cover was significantly lower than the reference site within Grass-removed-sow-plant ($p < 0.01$; Fig. 2.3; Table S4).

Of the plant species that were planted, more than 96% of species were still present within all treatments after one year. There was a significant reduction in species presence of planted species by the second year for all treatments ($p < 0.001$; Fig. 2.4A), except for Burn-sow-plant with an 81% survival. However, between the restoration treatments that excluded fire, there was no significant difference in the survival of planted species (Table S5). The overall species presence of sowed species was low, ranging from 9–16% for all treatments during the second year. During the second year, the species presence of sowed species was significantly higher within Soil-mulch-sow-plant (16%; $p = 0.01$; Fig. 2.4B; Table S6). Burn-sow-plant had the second highest presence of species sowed during the first year (19%) as well as the second year (12%).

2.4.2 Financial analysis

At R36,381/ha, the Burn treatment is the most cost effective (Table 2.2; Appendix A). When the cost of this treatment was scaled to 50 ha, the resources used largely remained the same, with a minimal increase in cost (Table 2.2). The costs of all other treatments showed a linear increase when scaled from 1 ha to 50 ha. At R422,791/ha, Remove-grass-sow-plant was the

most expensive. Burn-sow-plant (R234,172/ha) and Soil-plant (R153,594/ha) were estimated to have relatively moderate costs. Burn-sow-plant was identified as one of the most viable options, as it was most successful (highest native species richness) and had the fourth lowest cost (R234,172/ha) (Fig. 2.5). In terms of the treatments that involved the movement of soil and/or mulch, Soil-plant was the most successful treatment at a relatively moderate cost (R153,594/ha). Remove-grass-sow-plant had the least success and had the highest cost (R422,791/ha).
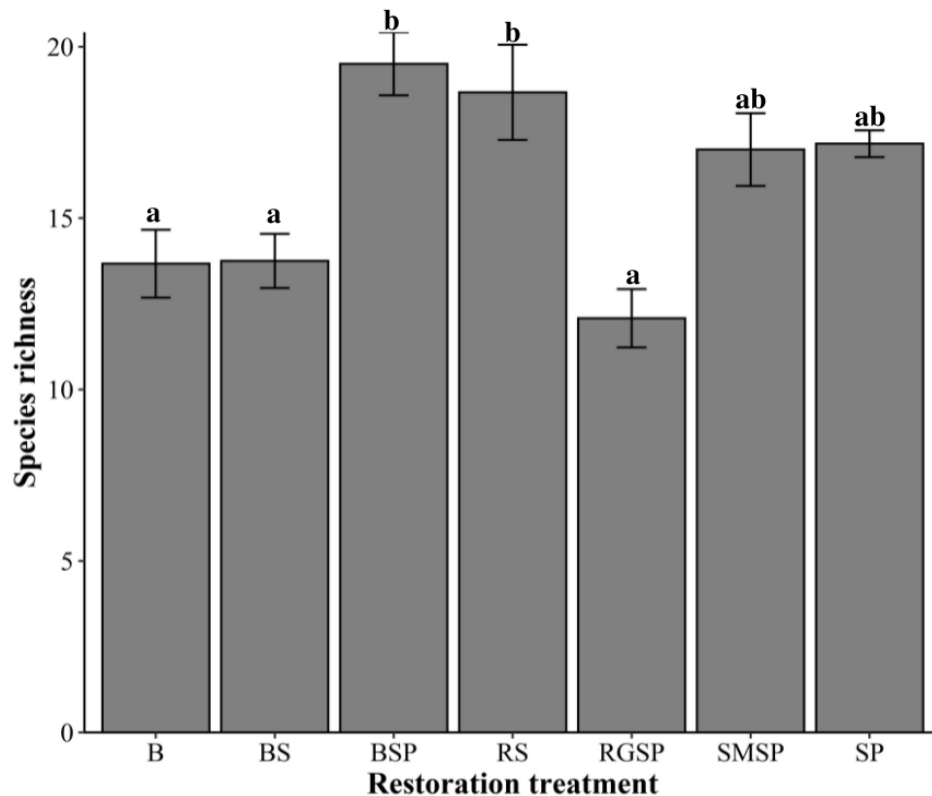
Figure 2.2 The effect of restoration treatment on native species richness (Generalized linear mixed models (GLMMs). Different letters above bars indicate significant differences between treatments where $p < 0.05$. Burn = B; Burn-sow = BS; Burn-sow-plant = BSP; Reference site= RS; Remove-grass-sow-plant = RGSP; Soil-mulch-sow-plant = SMSP; Soil-plant = SP.
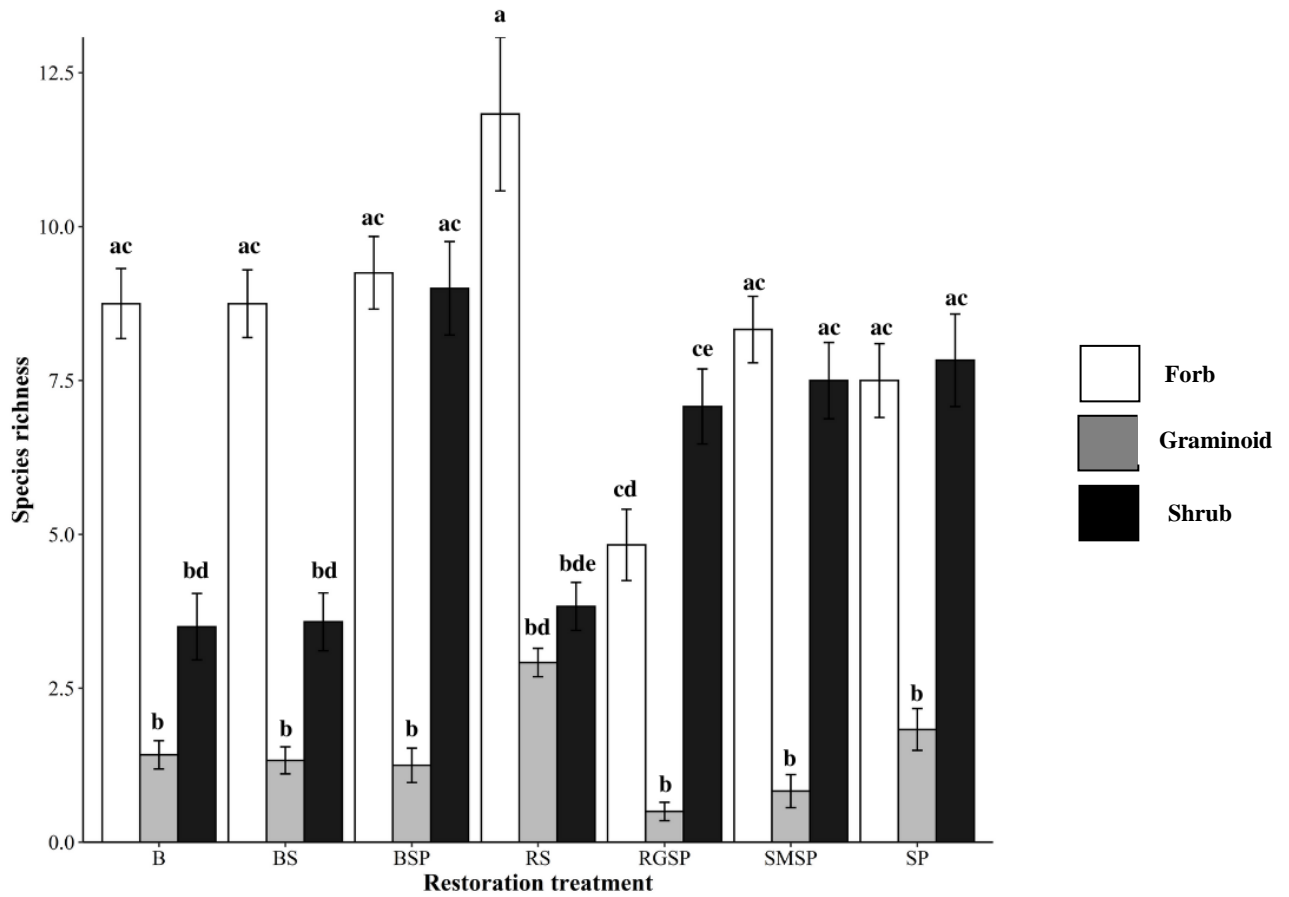
Figure 2.3 The effect of restoration treatment on native species richness per growth form (Generalized Linear Mixed Models (GLMM's). Burn = B; Burn-sow = BS; Burn-sow-plant = BSP; Reference site = RS; Remove-grass-sow-plant = RGSP; Soil-mulch-sow-plant = SMSP; Soil-plant = SP.
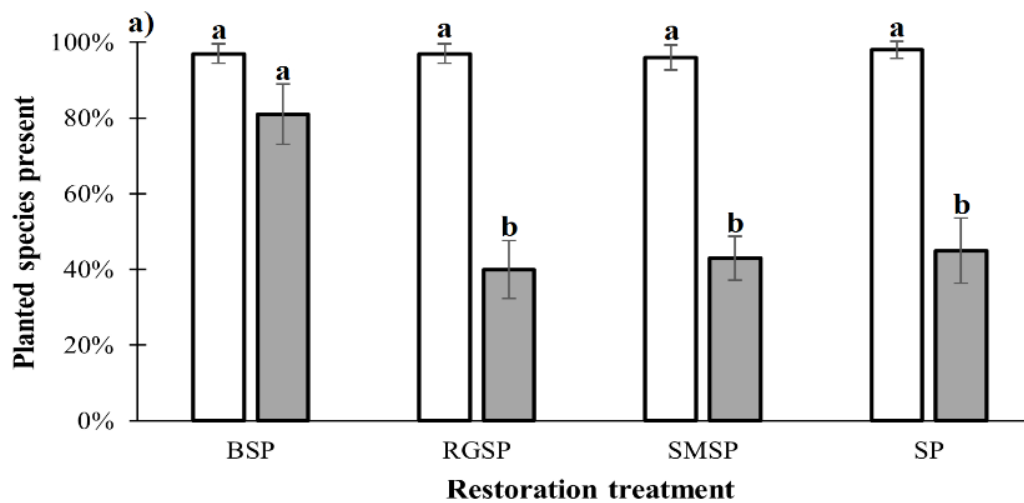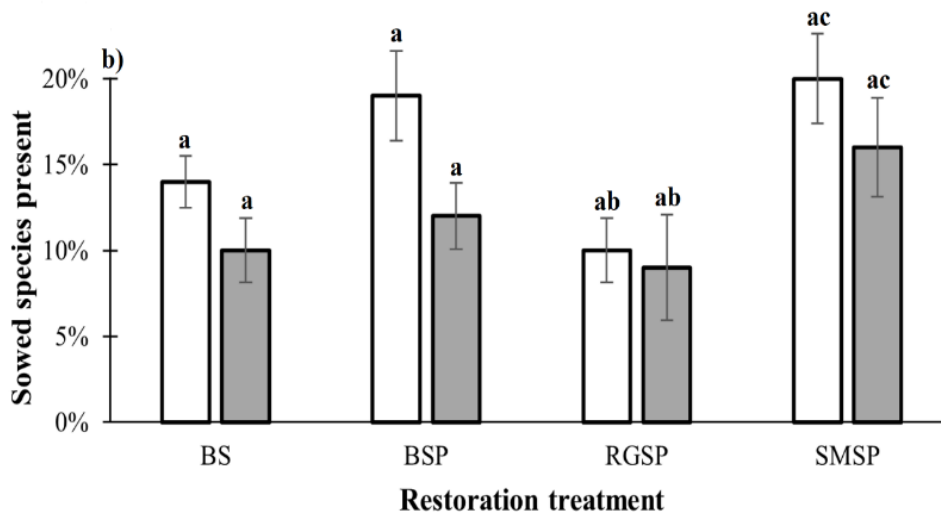
Figure 2.4 The percentage of planted (a) and sowed species (b) surviving in the different restoration treatments after 1 and 2 years. Burn = B; Burn-sow = BS; Burn-sow-plant = BSP; Remove-grass-sow-plant = RGSP; Soil-mulch-sow-plant = SMSP; Soil-plant = SP.
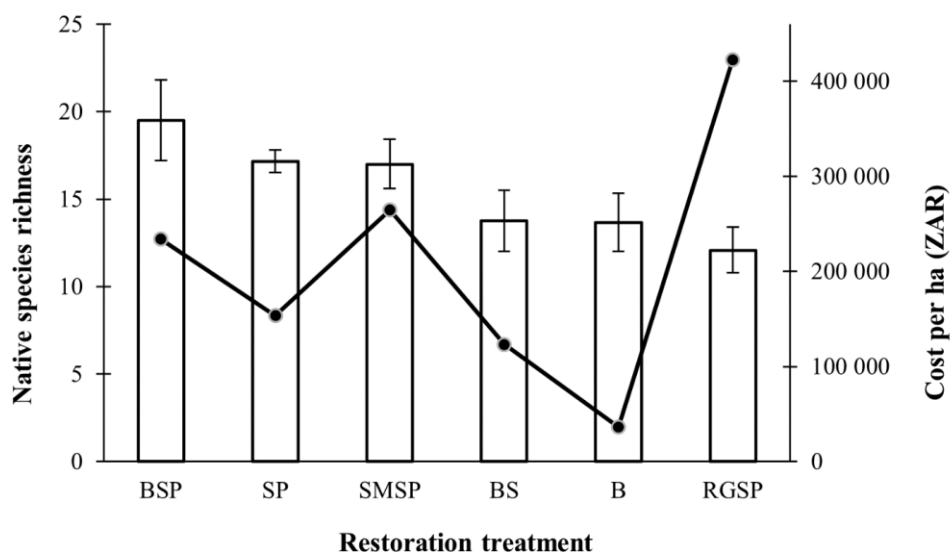
Figure 2.5 The success (indicated by bars) and costs (indicated by a line) of the six restoration treatments. Success is measured here as native species richness averaged across the 2 years post restoration. The cost of each restoration treatment was calculated by including all labour and resources required. Costs were calculated in South African Rands/ha (1 ZAR = 0.069 USD; 12 July 2021). Burn = B; Burn-sow = BS; Burn-sow-plant = BSP; Remove-grass-sow-plant = RGSP; Soil-mulch-sow-plant = SMSP; Soil-plant = SP.

Figure 2.6 Vegetation recovery 3 years after restoration. An aerial image of Site 2, 1 year prior to treatment application (a) is compared to an image of the area after topsoil translocation and mulch application to roads and parade rings (b). The Lost Site (c) is compared to the site where topsoil was translocated to (f). The initial condition of Site 1, where fire was applied (d) is compared to the condition of the site after treatment (e). Photos L. Retief.

Table 2.2 The combinations of restoration treatments used in this study and the cost/ha as well as cost/50 ha. Costs were calculated in South African Rands/ha (1 ZAR = 0,069 USD; 12 July 2021).

Restoration treatment	Cost/ha (ZAR)	Cost/50 ha (ZAR)
Soil-plant	R153,594	R7,679,700
Remove-grass-sow-plant	R422,791	R21,139,600
Soil-mulch-sow-plant	R264,696	R13,234,850
Burn	R 36,381	R55,951
Burn-sow	R 123,173	R4,395,551
Burn-plant-sow	R234,172	R9,945,551

2.5 Discussion

Here we show that fire combined with planting can restore plant species richness to that of a near-pristine reference site. We also show that the appropriate translocation of topsoil (with a soil seed bank) and subsequent planting can be successful in restoring Cape Flats Sand Fynbos (CFSF) communities. The exposure to heat and smoke from fire plays an important role in breaking the dormancy of seed and stimulating germination in fire-prone Mediterranean systems (Keeley, 2012; Hall et al., 2016; Holmes & Richardson, 1999; Kraaij & Van Wilgen, 2014). When fire is applied as an initial treatment, it assists in removing invasive grass layers and exposing soil for successful sowing and planting in the absence of competition (Holmes, 2008). In a restoration study done by Waller (2013), it was evident that the use of fire alone with no other restoration treatments kept native species richness relatively low. This is consistent with our study – not only for Burn, but also for Burn-sow.

Although the presence of sowed species was slightly higher when used in combination with fire and planting (Greet et al., 2020) as well as the application of mulch, sowing had no significant effect on restoration success. This seemingly low contribution of pre-treated seeds sowed after the fire is in contrast with the findings of Hall et al. (2016), whose results showed this to be a successful combination of restoration treatments. While our results correspond with those of Gaertner et al. (2012), where the application of seed had no significant effect on native species richness, both these two studies applied fire following the clearing of the woody alien invasive species, *Acacia saligna* (Port Jackson willow). In contrast, prior to restoration, woody alien plants species such as *A. saligna* were absent from our study site, which resembled an old agricultural field with mostly alien grass species present.

The relatively high survival rate of planted species in our study, as opposed to sowed species, supports the notion of the importance of nurse plants providing shelter to emerging seedlings (Padilla & Pugnaire, 2006; Ruwanza, 2019). It has also been found that with sowing alone, it

takes long for larger shrub species to establish themselves (Homes & Richardson, 1999). Thus, the inclusion of planting can ensure a high native shrub cover. Fire reduces competition posed to newly planted plants (Holmes, 2008), while it also acts as an important mineralizing agent offering a post-fire flush of nutrients made available (Stock & Lewis, 1986; Le Maitre & Midgley, 1992; Cowling et al., 1997). This may explain the higher survival rate of planted species in the burnt treatment.

Sowing within mulched areas can assist germination of seed by providing shelter and moisture (Rokich et al., 2002; Pretorius et al., 2008; Benigno et al., 2013), which corresponds with our results. However, we did not test the factors that could have affected the overall low germination of sowed species. These factors could have included a lack of germination cues or other environmental factors such as the prevailing weather conditions. Furthermore, it could have been due to direct competition with alien grass species (Waller et al., 2016; Nsikani et al., 2020) since within treatments that did not include the application of topsoil, the invasive grass, *Avena fatua,* was abundant. The leachate of *A. fatua* is known to have an allelopathic effect on the germination of seeds (Tinnin & Muller, 1972). The low success rate of the Remove-grass-sow-plant treatment could possibly be due to the high remaining grass component within the surrounding habitat of treatment plots, that were still distributing seed into the plot area. Alien grass species grow faster than native plants (Ruwanza, 2017) and can produce a high quantity of seed. There is a possibility that a number of the existing native seeds could have been removed with the invasive grass layers or that the results here are linked to the features of the tested site itself, which had a very distinct history of alien grass species being present.

The success of topsoil translocation can depend on the containing of an adequate seed bank within the soil (de Villiers et al., 2004; Buisson et al., 2018), which is why it is recommended that topsoil application must be used with other restoration techniques (Fowler et al., 2015; Pilon et al., 2019). Studies have shown that topsoil translocation can be successful in suppressing a seed bank of invasive weeds and grass species (Koch, 2007b; Ruwanza, 2020). Due to topsoil having been translocated from near-pristine site, we could test the method in the absence of a large seed bank of either grass or weed species, which reduced overall competition with native species. Simultaneously, the translocated topsoil could provide optimum conditions for the successful rooting of plants due to soil structure and soil processes having been in place (Holmes, 2001). Using a combination of planting with topsoil translocation, successfully facilitated the restoration of a native plant community, including native shrub cover, and a system that resembled the area that was lost. Holmes (2001) found a high native species richness within areas that received topsoil application with sowing, even though certain plant species which are important key structural elements in the vegetation

type were still missing. This could potentially be addressed by incorporating the planting of selected plant species as a restoration factor. The treatment Soil-plant was the only treatment where *Muraltia satureioides* was present, a species that was found in the lost site and was moved as seed within the translocated topsoil. This species is part of the Polygalaceae family, a taxon known to be problematic to cultivate (Nichols, 2005). Topsoil translocation does not constitute adequate mitigation for the loss of endangered habitat (Bullock, 1998), nor does it replace in situ conservation (Jaunatre et al., 2014). However, it could be seen as a means to relocate and introduce plant species that are difficult to cultivate from either seed or vegetative cuttings.

Approximately 75% of the native species that were present in the lost site, were successfully restored in the restoration site. We recommend that species introduction efforts continue over the long term, since important structural elements are still missing. These are particularly important for ecosystem function such as pollination (Geerts, 2011; Geerts et al., 2020), in particular in small urban reserves (Mnisi et al., 2021). We also encourage further introduction of rare plant species that were present in the lost site and were either absent or only present as single individuals after restoration, since the absence of key structural components can delay faunal recover extensively (Geerts et al., 2016; Mangachena et al., 2019). Our results only represent data collected for 2 years after restoration treatments, which is relatively short-term for restoration studies in Fynbos (Holmes, 2005; Hall et al., 2021) and Mediterranean systems in general (Vallejo et al., 2012). The lack of success with some of our restoration treatments tested may have been due to one of the worst droughts in recent history that was experienced in the region during the three years prior to restoration treatments taking place (Padilla et al., 2009; Archer et al., 2019) or competition with alien grasses (Holmes, 2008). It is unlikely that the low success rate of some treatments was due to herbivory or granivory, since antelope were excluded from our study area by a fence and no rodent activity or excessive activity of other granivores, such as ants, was noted. Our findings are in contrast with those of Midoko-Iponga et al. (2005) and Maron and Simms (2001) where no exclusion measures were used. This is important since herbivores are known to influence restoration success - even more so after a fire (Godefroid et al., 2011). Long-term methods of exclusion in restoration sites such as done here should be considered to enhance restoration success (Silva et al., 2015). However, such long-term enclosures add to the expenses of a restoration project.

Similar to Waller (2013), we found that the number of factors included in our restoration treatments corresponded positively with the cost, but the most successful treatment was not necessarily the most expensive. We carried out restoration treatments with methods that were suited to a small-scale urban restoration project. In larger areas, mechanized options could

be used which could be more cost-effective (Holmes & Richardson, 1999; Campos-Filho et al., 2013; Navarro-Pedreño et al., 2017). Despite this, the relative difference in cost between all the tested restoration treatments should remain constant, even at other restoration sites. Burn-sow-plant proved to be the most successful treatment, but also more expensive relative to Burn and Burn-sow. It is widely known that the use of seed in restoration projects is cheaper than planting (Greet et al., 2020; Ruwanza et al., 2013; Hall et al., 2021), but we show here that the added success achieved by including planting, allows restoration practitioners to weigh costs against success.

Burn was the only restoration treatment that did not show a linear increase in terms of cost. The concept of economy of scale became relevant since, as the size of the burn area is increased to a scale larger than 50 ha, the cost per hectare comes down (Jackson et al., 1982). Soil-plant was far less expensive and more successful than Soil-mulch-sow-plant, regardless of the addition of mulch and seed to the latter, which also did not contribute to restoration success. The high cost of the Soil-mulch-sow-plant treatment was primarily due to the labour necessary for mulch application, seed collection and sowing. In contrast, topsoil application can be applied in a shorter time with less labour needed (Koch, 2007b). This is a cost-effective restoration treatment which is suited to Mediterranean systems with high levels of biodiversity, where technical knowledge of germination treatments and propagation are often limited (Fowler et al., 2015). However, we must acknowledge that topsoil transfer is only applicable to specific situations, where the integrity of small conservation sites is compromised. The viability of topsoil translocation as part of large-scale restoration projects as well as a restoration factor tested without other interventions such as planting will have to be explored. The most expensive and least successful treatment was Remove-grass-sow-plant. The method was time-consuming and ultimately amounted to high costs. These high costs associated with the method of removal with spades corresponded with that of hand-clearing methods used by Musil et al., (2005). In said study it was found that the most cost-effective method to reduce alien grasses was to apply mowing before the grasses set seed. However, this would not have reduced the weedy stoloniferous grasses on our study site (Holmes, 2008). The challenging removal of these grass species and the high costs associated with it, emphasize the importance of the use of fire for the restoration of Mediterranean systems to reduce the competition posed by invasive alien grass.

In conclusion, we recommend that, with limited funds, the application of fire is used. Where an extensive budget is available, the use of fire in combination with planting is advised. In unique situations where the loss of small intact natural areas – with an intact native seedbank – is unavoidable, the translocation of topsoil in combination with planting can be successful, even with a moderate budget.

2.6 Implications for practice

When scaling up restoration initiatives, fire remains one of the most cost-effective options for restoration in Mediterranean systems, and works well in synergy with other treatments, which enhances restoration success rates. While sowing as a restoration treatment is cheaper and easier to scale up, the effect of planting can greatly improve the success of restoration attempts in terms of survival of the introduced plant species as well as restoring native shrub cover. The translocation of topsoil from near-pristine sites, combined with the planting of propagated plants is a cost-effective method despite the absence of fire. Where the impact of development is unavoidable, or where the integrity of very small conservation sites is compromised, the option of topsoil translocation should be investigated as a last resort. We carried out restoration treatments with methods that were suited to a small-scale urban restoration project. In larger areas, mechanised options could be used which could be more cost-effective by reducing the costs of labour. The application of fire and topsoil translocation from near-pristine sites respectively aids in reducing competition from alien species.

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CHAPTER THREE

ACTIVE RESTORATION IN A SMALL URBAN RESERVE LEADS TO PARTIAL POLLINATOR RECOVERY

3.1 Abstract

Pollinator visitation can ensure the long-term success of vegetation restoration, as it will prevent the eventual decline of introduced plant species by ensuring their reproduction and genetic variability. Even though the importance of also restoring pollinators has been emphasized, few studies quantify restoration success in terms of ecosystem function. Over a period of two years, I tested how successful pollination is restored by an active plant-focused restoration approach. By comparing a recently restored site with two reference sites (fragmented and intact) in the Fynbos of South Africa, I aimed to determine whether pollination was restored by comparing the visitation frequency and species richness of pollinators. I also determined seed set of generalist and specialist pollinated plant species. While the pollinator species richness and visitation frequencies for some generalist plant species were either higher within the fragmented site or the same for all three study sites, the majority of generalist plant species had the most pollinator visits within the intact site (1.3–9.6). Specialist plants that were incapable of autonomous selfing was absent from fragmented study sites and when introduced at these sites, pollination was still sub-optimal. Natural seed set for generalist plant species indicated optimal pollination at all sites. My results show that generalist plant species have a greater potential to facilitate ecosystem recovery in terms of pollination. In contrast, the restoration of specialist plant species may not work in the long-term due to a lack of pollinators within small urban fragments. However, providing sustained nectar sources and stepping-stones for specialist pollinators might aid in enhancing ecosystem function in small urban nature reserves.

3.2   Introduction

Plant-pollinator mutualisms date back to the Cretaceous period when insect activity started to increase the reproductive success of plant species (Sánchez-Bayo & Wyckhuys, 2019). Plants are static organisms that must either rely on autonomous selfing (vector-less self-pollination) (Rodger & Ellis, 2016), or on having pollen carried by vectors such as wind, water, or animals (Ollerton, 2017). About 90% of flowering plants worldwide are reliant on pollination for reproduction and maintaining genetic variability (Menz et al., 2011). Consequently, the dependence of plants and pollinators on each other for survival is of high ecological importance (Ollerton et al., 2011), as pollinators receive pollen, nectar, or oil from the plant -

and the plant receives a pollination service for reproduction in return (Michener, 2000; Johnson, 2010).

Plant species form important mutualistic relationships with pollinators as keystone species which, if lost, will lead to the collapse of plant-pollinator networks (Gilbert, 1980). Furthermore, pollen limitation may lead to a decreased seed set (Bond, 1994) which, in turn, can lead to the decline of plant populations (Ashman et al., 2004). According to Bond (1994), the two major risks of extinction to plants are the failure of pollination, as well as the sole dependence of plants on pollination for reproduction. Although plant species that can self-pollinate and are not solely dependent on pollinators, are known to survive better (Baker, 1965), the risk of inbreeding depression leads to a higher risk of extinction (Igic et al., 2008; Ollerton, 2017).

While a specialist pollinator might rely entirely on one plant species for pollen, the plant species may still be visited by a wide array of other pollinators, making it a generalist in terms of pollination (Waser et al., 1996). However, plants with specialized pollination systems that are pollinated only by a single or a small number of pollinator species (Johnson & Steiner, 2000) may be more at risk of extinction (Pauw, 2007). Generalist pollinators use a wider range of resources; therefore, they are far less affected by threats such as urbanization (Wenzel et al., 2020) and fragmentation which can decrease pollen resources and nesting habitat (Donaldson et al., 2002). Because generalist plant species can exploit the remaining available pollinator community, they may be minimally affected by fragmentation or degradation (Waser et al., 1996). Although generalist plant species receive pollination visits from a wide array of species (Johnson & Steiner, 2000), a possible decline of generalist pollinators can eventually also lead to a decline of the specialist plant species in the network (Pauw, 2007).

Tewksbury et al. (2002) attributes the effect of fragmentation on animals to patch size, edge effects, and landscape connectivity. While patch size can influence the local extinction of populations as a certain number of individuals is needed to survive environmental fluctuations, edge effects may influence reproduction. The connectivity of the area to other natural areas will also determine the rate of dispersal and colonization of populations (Hadley & Betts, 2012). Recent evidence clearly shows pollinators and associated plant species that are dependent on them are globally in decline (Potts et al., 2010; Sánchez-Bayo & Wyckhuys, 2019; Zattara & Aizen, 2021). Pollination is negatively affected by anthropogenic disturbances such as habitat fragmentation (Donaldson et al., 2002; Garibaldi et al., 2011; Neuschulz et al., 2016; Delnevo et al., 2020), because the structure and stability of plant and pollinator communities may be less in isolated remnants (Cusser et al., 2013). In the urban context, fragment sizes are often small, with increased degradation in the surrounding landscape (Fahrig, 2017). Therefore, pollinators in these areas are vulnerable to extinction, with no prospects of re-

colonization (Garibaldi et al., 2011). Furthermore, pollinator richness and stability decrease with increasing distance from well-protected natural habitat (Carvalheiro, 2010; Garibaldi et al., 2011). Eventually, fragmentation and associated land degradation can lead to a decrease in floral resources, pollinator richness and abundance, which has the potential to change the biotic interactions in these areas (Gonza´lez-Varo et al., 2013).

The degradation of land is usually associated with reduced native plant species richness (Rebelo et al., 2011), which can affect the diversity and stability of pollinators (Ebeling et al., 2008; Johnson, 2004) due to a reduction in floral abundance and a consequent lack of food for pollinators (Kearns & Inouye, 1997), especially those which are specialist pollinators (Pauw, 2007). Evidence suggests that pollinator communities can be successfully restored in vegetation restoration sites such as meadows (Forup & Memmott, 2005), British heathlands (Forup et al., 2008), prairie (Ritchie et al., 2020) and forests (Kaiser-Bunbury et al., 2017). While species richness and visitation frequencies of pollinators can provide insight into plant-pollinator interactions in restoration sites (Williams, 2011) and whether plant species are generalists or specialists (Pauw & Stanway, 2014), these factors do not necessarily indicate successfully restored pollination (Breland et al., 2018). By including pollen supplementation experiments, which provide insight into pollen limitation and to what degree pollen limits seed set, conclusions can be drawn from the sum of all factors, rather than each individual data set (Knight et al., 2005). However, few studies have considered pollen limitation as part of measuring restoration success (but see Pan et al., 2017; McCallum et al., 2019; Ritchie et al., 2020). Furthermore, there still is a general paucity of research in terms of the integration of plant restoration results and pollination (Menz et al., 2011) in Mediterranean-type habitats such as South African Fynbos (but see Geerts et al., 2020; Mnisi et al., 2021).

Fynbos is a vegetation type that is unique and limited to the Cape Floristic Region (CFR) in South Africa. The region is characterised by a Mediterranean climate (Rebelo et al., 2006) and has an exceptionally high level of plant diversity and endemism (Manning & Goldblatt, 2012). As plant diversity is a good predictor of insect diversity across spatial scales, (Proches & Cowling, 2006; Proches et al., 2009; Kemp & Ellis, 2017) specialization of pollination systems in areas such as these are also high (Johnson & Steiner, 2004; Johnson, 2004; Pauw & Stanway, 2014; Geerts et al., 2020). Furthermore, in stark contrast to the rest of the world, only four specialist bird pollinators occur throughout the CFR (Geerts et al., 2020). These four bird species represent a group that pollinates 4% of the total number of plant species in the region (Rebelo, 1987).

In areas with a high degree of plant and pollinator specialization, plant-pollinator relationships would be difficult and complex to restore, should specialists become extinct (Menz et al.,

2011). However, few studies have included pollination as an ecological function to be evaluated as part of active vegetation restoration programmes (Acosta et al., 2018, Genes & Dirzo, 2022), as restoration programs consider plant survival and not reproduction (Godefroid et al., 2011). Pollination processes may not automatically be reinstated with the return of target plant species, although it is crucial for the sustainability of restoration projects (Forup & Memmoth, 2005), even more so in severely fragmented and critically endangered habitats. Consequently, pollination can be used as a measure to assess restoration success (Forup et al., 2008) and to ascertain whether key species linkages have been reinstated or not (Ehrenfeld & Toth, 1997).

Here I aim to test whether active vegetation restoration is successful in restoring pollination as an ecosystem function, which can influence the survival of restored plant species in the long-term. Specifically, I addressed the following questions: 1) how does pollination in a recently restored site compare to that in a fragmented and intact natural site? 2) Is seed production suboptimal in restored sites? 3) Is the reproduction of plant species pollinated by specialist pollinators compromised in recently restored areas?

3.3   Methods

3.3.1 Site selection and study area

The study area was located within Table Bay Nature Reserve, an urban nature reserve in Cape Town, in the Cape Floristic Region (CFR) of South Africa (Fig. 3.1). The Table Bay Nature Reserve consists of multiple natural areas that are managed as conservation sites, although not all of them are connected. Three of these sections made up the experimental sites for this study. These included a 3ha recently restored fragment (from here on referred to as the Restored Fragment), a 19ha near-pristine but fragmented site (from here on referred to as the Nature Reserve Fragment), and an 600ha intact site (from here on referred to as the Nature Reserve Intact) (Fig. 3.1).

An active restoration project took place within the Restored Fragment, six months before data collection started. The area consisted of critically endangered and degraded Cape Flats Sand Fynbos, which was primarily invaded by invasive alien grasses. The Nature Reserve Fragment, as well as the Nature Reserve Intact were both near-pristine sites of respectively, critically endangered Cape Flats Sand Fynbos and endangered Cape Flats Dune Strandveld with smaller patches of Cape Flats Sand Fynbos.

The Restored Fragment was used as experimental site and is directly adjacent to the Nature Reserve Fragment. The Nature Reserve Fragment and the Nature Reserve Intact were used as reference sites. The Nature Reserve Intact is located 500m away from the Restored

Fragment and the Nature Reserve Fragment. No natural corridors for the dispersal of pollinators exist in between as it is separated by housing developments, as well as several municipal and provincial roads.
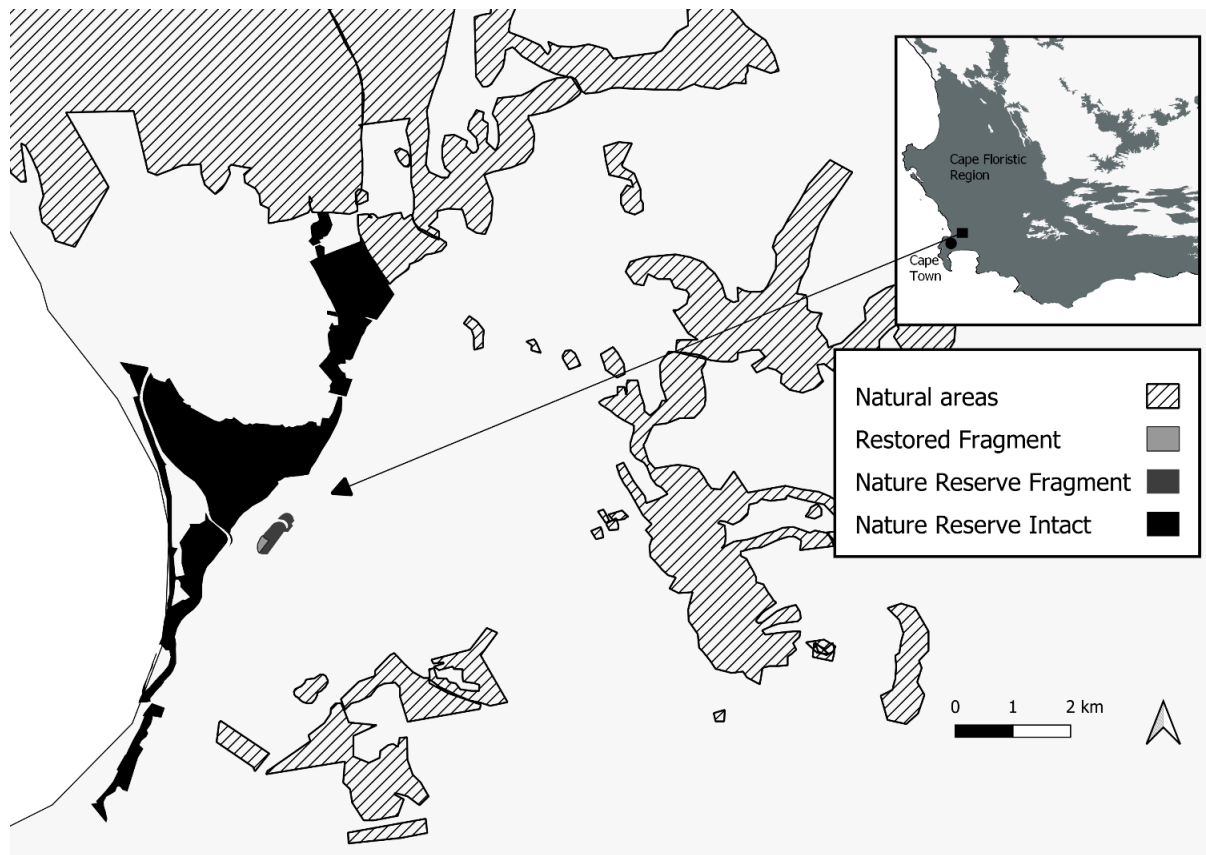
Figure 3.1: The study area was located within Table Bay Nature Reserve (indicated by the grey and black), an urban nature reserve in Cape Town, in the Cape Floristic Region (CFR), South Africa. The site was divided into the following three areas - Restored Fragment; Nature Reserve Fragment and Nature Reserve Intact. The remaining natural areas around the study site is also indicated. *Right inset* The extent of the CFR as well as the location of Table Bay Nature Reserve.

3.3.2 Study species

Plant species included in experiments were *Ferraria crispa, Moraea flaccida, Ornithogalum thyrsoides, Trachyandra divaricata* and *Babiana tubiflora,* which were present at all three study sites as large populations. Plant species that were absent or present only in low numbers within the experimental site or any of the two reference sites, were supplemented in containers with water. These were, *Watsonia meriana (*for which approximately 50 inflorescences were supplemented at the Restored Fragment and the Nature Reserve Intact) and *Brunsvigia orientalis* (for which approximately 50 inflorescences were supplemented at the Restored Fragment and the Nature Reserve Fragment).

Flowers of *F. crispa* (Iridaceae) have a distinct smell that is known to attract pollinators in the order Diptera (Goldblatt et al., 2009). *M. flaccida,* a geophyte within the Iridaceae family, has been found to be capable of autonomous selfing (van Kleunen et al., 2008). Likewise, *O. thyrsoides* (Hyancinthaceae) is a geophyte, which has also been found to produce seeds by autonomous selfing, (Donaldson et al., 2002). Previous research performed on *Trachyandra hirsuta,* indicates that the species is not capable of autonomous selfing (Donaldson et al., 2002). *B. tubiflora* (Iridaceae) is a geophyte of which the lower part of the perianth tube of flowers is elongated to approximately 80mm. This specialist plant species is known to only be pollinated by the long-proboscid fly, *Moegistorhynchus longirostris* (Goldblatt & Manning, 2007). *Nectarinia famosa* (Malachite Sunbirds) are the only known pollinators of *W. meriana*, making it a specialist in terms of pollination (Geerts & Pauw, 2009). Pauw (2004) found that specialist plant, *B. orientalis* (Amaryllidaceae), is not capable of autonomous selfing and that the two sunbirds, *N. famosa* (Malachite sunbird) and *Nectarinia chalybea* (Lesser Double-Collared Sunbird), are solely responsible for pollination of the species.

3.3.3 Pollinator observations

To assess if active vegetation restoration alone facilitates the return of pollinators, flower visitor observations were conducted. Observations were done over multiple days to compare pollinator species presence and visitation frequency between the three study sites. Observations were carried out during the months that plant species were flowering. All species flowered in spring, except *B. orientalis*, which flowered in autumn.

Individual observation periods for insects went on for 20 minutes. Plant species known to be pollinated by insects (*T. divaricata, F. crispa, B. tubiflora, O. thyrsoides, M. flaccida)* were watched from a distance of 2–5m. Individual observation periods for birds lasted for 30 minutes. Observations of bird pollinated plants (*W. meriana* and *B. orientalis*) were done within a fixed 50m radius. A two-minute resting phase after the observer sat down was allowed for bird species to settle and resume their natural behaviour.

Only observed visits where contact with the anthers or the stigma of a flower was made were recorded as pollination, to distinguish between those pollinators that were only visitors and those that were perceived to be pollen vectors. A total of 3 hours of pollinator observations were done per plant species, per site, totalling 9 hours per plant species. Observations were carried out on days that had ideal and similar conditions for pollinators such as dry, sunny days with no more than moderate wind speeds (Forup & Memmott, 2005) and was limited to day-visiting pollinators. To control for different numbers of flowers observed, the number of visits, per flower, per hour was recorded (Moodley et al., 2016). Different floral compositions and abundance between the sites could influence pollinators. Therefore, the floral

neighbourhood at all observation sites was quantified by recording the number of open flowers present that were observed for insect visits, as well as all open flowers within an approximate 10-meter radius around the observed flowers. This radius was extended to approximately 50-meters during observation sessions that focused on bird pollinated plant species. Only floral numbers of plant species that would be visited by the observed pollinator group were included, which were either insect or bird pollinated plant species.

Pollinator species that were recorded were identified at least up to family level (Table S7) and were grouped into functional groups that have similar behaviour (Fenster et al., 2004; Whitehead et al., 1987). Plant species with pollinators from three or more functional groups were classified as generalists, while those with pollinators from less than three functional groups were classified as specialists (Brosi, 2016). All bird-pollinated plant species were regarded as specialists.

3.3.4 Seed set

To test if pollination was optimal or sub-optimal, we aimed to test if seed production was limited and to what extent. Flowers were used for experiments on *Ferraria crispa, Moraea flaccida, Ornithogalum thyrsoides, Trachyandra divaricata* and *Babiana tubiflora*, while inflorescences were used for those of *Watsonia meriana* and *Brunsvigia orientalis*. i) To test if plant species are autonomous and to what extent, pollinators were excluded with gauze bags when flowers/inflorescences were still in bud (autonomous); ii) A flower/inflorescence on the same plant was marked as part of a control group and left open to be naturally pollinated (natural); and iii) For pollen supplementation, another flower/inflorescence on the plant was left open, and pollen was supplemented by hand once the buds opened (pollen supplemented), which could indicate whether pollination under natural conditions were optimal or sub-optimal (Ashman et al., 2004). Experiments were done on 10-12 plants of each plant species per site, with all three experiments being performed on 1-2 flowers or inflorescences per plant for *Ferraria crispa, Trachyandra divaricata, Watsonia meriana* and *Brunsvigia orientalis*. Due to the anatomy of *Moraea flaccida, Ornithogalum thyrsoides* and *Babiana tubiflora,* experimental sets of three were performed on more than one plant for these species.

For pollen supplementation, an anther from another non-specific plant of the same species, at least 10m away, was brushed across the stigmatic surface of receptive flowers. Only inflorescences with almost all flowers open and with older flowers still receptive (stigma not shrivelled) were selected (Geerts, 2016). For smaller flowers, pollen sticking to the stigma after supplementation was confirmed with a hand lens. For those plant species that had flowers of which the stigma was receptive for one day only, pollen was supplemented once. For those of which the stigma was receptive for more than one day, pollen was supplemented

twice, on the same stigma, but on different days. After fruit set occurred, the amounts of seed in each fruit were counted by hand. The potential maximum seed set was determined within the group that received pollination supplementations. Even though data on fruit set was not recorded, all flowers and inflorescences used for experiments produced capsules, whether they produced seeds or not. Seed set data on *W. meriana* at the Nature Reserve Intact had to be excluded from the results, due to the fact that the experimental plants were left without water for an extended time after very strong wind in the study area.

3.3.5 Statistical analyses

3.3.5.1 Pollinator species richness

All statistical analyses were performed in R version 4.0.3 (R Development Core Team 2020). The effect of state of the study site (Restored Fragment, Nature Reserve Fragment and Nature Reserve Intact) on pollinator species richness of *F. crispa*, *M. flaccida*, *O. thyrsoides*, and *T. divaricata* was investigated by fitting generalized linear models (GLM). In all study sites, species richness was zero for *B. tubiflora*, *W. meriana* and *B. orientalis*, therefore, these species were excluded from the analysis. Due to species richness being positive count data (integers), the distribution of GLM errors as Poisson-distributed was initially considered. Over-dispersion of the GLMs was then checked using the function *dispersiontest* of the *AER* package (Kleiber & Zeileis, 2008) and detected for all species except *T. divaricata*. Therefore, Poisson models were discarded and Quasi-Poisson models fitted instead. Significant mean differences were separated with Tukey's HSD (Honest Significant Difference) test using the *emmeans* package (Lenth, 2018).

3.3.5.2 Visitation rate

The effect of state of the study site (Restored Fragment, Nature Reserve Fragment and Nature Reserve Intact) on the visitation rate of pollinators on *F. crispa*, *M. flaccida*, *O. thyrsoides*, and *T. divaricata* was investigated by fitting linear models for each species. The effect of floral neighbourhood on the visitation rate had no significant effect and was therefore excluded from further analyses (Table S8). Residual and Q-Q plots were computed to check for data normality. Significant mean differences were separated with Tukey's HSD test using the *emmeans* package (Lenth, 2018).

3.3.5.3 Seed set

The effect of pollination treatment (natural, pollen supplementation, autonomous) and state of the study site (Restored Fragment, Nature Reserve Fragment and Nature Reserve Intact) on the seed set of *B. tubiflora*, *M. flaccida, O. thyrsoides* and *T. divaricata* was investigated by fitting generalized linear models (GLM). Due to seed set being positive count data (integers),

the distribution of GLM errors as Poisson-distributed were initially considered. Over-dispersion of the GLMs was then checked using the function *dispersiontest* of the *AER* package (Kleiber & Zeileis, 2008). In the case of seed set for all study species, over-dispersion was detected. For *B. tubiflora* and *O. thyrsoides*, overdispersion was due to an excess of zeros in the data; thereby, suggesting zero-inflation in the dataset. Therefore, Poisson models were discarded and zero-inflated models fitted instead. The zero-inflated models were fitted using *pscl* package (Zeileis et al., 2008). Due to the presence of limited zeros and over-dispersion in the *M. flaccida* and *T. divaricata* seed set data, Poisson models were discarded and Quasi-Poisson models fitted instead. For *F. crispa*, *W. meriana* and *B. orientalis*, seed set per capsule data for each species was log transformed to follow a normal distribution. Residual and Q-Q plots were computed to check for data normality. The effect of pollination treatment and state of site on seed set per capsule for each study species was then determined through a two-way Analysis of Variance (ANOVA). Significant mean differences were separated with Tukey's HSD test using the *emmeans* package (Lenth, 2018).

3.4 Results

3.4.1. Pollinators

In terms of specialization, *Ferraria crispa*, *Moraea flaccida*, *Ornithogalym thyrsoides* and *Trachyandra divaricata* were classified as generalists, as each of these had pollinator species visits out of three or more functional groups. Even though no pollinator visits were recorded for *Babiana tubiflora, Watsonia meriana and Brunsvigia orientalis,* these were classified as specialist species according to available literature (Table 3.1). Pollinator visitation on generalist plant species was significantly higher within the Nature Reserve Intact for two of the four tested species (1.3 –1.6). The average pollinator species richness of visitors to generalist plant species was 41-59% lower at the Restored Fragment and the Nature Reserve Fragment than the Nature Reserve Intact. There was a significant interaction between the effect of specialization and site state on visitation rate as no pollinator visits were observed on any of the tested specialist plant species at any of the study sites (Table 3.1).

A total of 16 insect taxa from 11 families were recorded as pollinator visitors to generalist plant species, with the highest number of 13 species from 9 families within the Nature Reserve Intact (Table S7). For *F. crispa*, 83% of pollinator visitors were Dipterans (Table S9). Pollinator species richness for *F. crispa* was significantly higher in the Restored Fragment than the Nature Reserve Fragment and the Nature Reserve Intact (4.2; p < 0.001; Table 3.1). Pollinator visitation rates of *F. crispa* within the Nature Reserve Intact was significantly lower than the Nature Reserve Fragment (p = 0.008; 71%), while there was no significant difference between visitation within the Restored Fragment and the Nature Reserve Fragment (p = 0.09; Table

3.1). Pollinator species richness was significantly lower at the Restored Fragment (71-100%; Table 3.1) for *M. flaccida* (p = 0.008) and *O. thyrsoides* (p = 0.04). Pollinator visitation was also significantly lower within the Restored Fragment for *M. flaccida* (p = 0.01; 86-100%; Table 3.1) and *O. thyrsoides* (p = 0.007; 86%; Table 1). For *T. divaricata* there was no significant difference between the pollinator species richness or pollination rate between study sites (Table 3.1). *Apis mellifera capensis* accounted for 97% of pollinator visits on *T. divaricata* (Table S9).

Table 3.1: A summary of pollinator species richness and visitation frequency as well as the specialization of the studied plant species including the functional groups that were observed as pollinators. The range of pollinator species richness is indicated within brackets. Visitation frequency is expressed as the number of visits, per flower, per hour. Superscript letters indicate significant differences. Plant species with pollinators out of three or more functional groups were classified as generalists, while those with pollinators out of less than three functional groups were classified as specialists. All bird-pollinated plant species were regarded as specialists. If no pollinators were observed on a plant species during the study, but the specialization level was widely known by previous research, it was classified according to the relevant published literature. RF = Restored Fragment NRF = Nature Reserve Fragment NRI = Nature Reserve Intact.

Plant species	Species richness			Visitation frequency			Specialization	Functional groups (Whitehead et al.,1987)
	RF	NRF	NRI	RF	NRF	NRI		
F. crispa	$4.2 (2-6)^a$	$1.9 (1-4)^b$	$3.7 (0-3)^b$	$18.8 (\pm19.3)^{ab}$	$33.5 (\pm17.9)^b$	$9.6 (\pm12.5)^a$	Generalist	Long-tongue bees; Flies; Carrion flies
M. flaccida	0	$0.1 (0-1)^a$	$1.6 (0-4)^b$	0	$0.2 (\pm0.6)^a$	$1.6 (\pm1.8)^b$	Generalist	Long-tongue bees; Short-tongue bees; Flies; Beetles
O. thyrsoides	$0.6 (0-1)^a$	$1.1 (1-2)^{ab}$	$2 (1-4)^b$	$0.2 (\pm0.2)^a$	$1.2 (\pm0.9)^b$	$1.3 (\pm0.8)^b$	Generalist	Long-tongue bees; Short-tongue bees; Beetles; Flies; Settling moths; Carrion flies
T. divaricata	$1.1 (1-2)^a$	1^a	$2.7 (1-3)^a$	$14 (\pm8.2)^a$	$8.7 (\pm6.3)^a$	$5 (\pm2.7)^a$	Generalist	Long-tongue bees; Short-tongue bees; Carrion flies; Flies
B. tubiflora	0	0	0	0	0	0	Specialist (Goldblatt & Manning, 2007)	Long-proboscid flies
W. meriana	0	0	0	0	0	0	Specialist (Geerts & Pauw, 2009)	Perching birds
B. orientalis	0	0	0	0	0	0	Specialist (Pauw, 2004)	Perching birds

3.4.2 Seed set

Average natural seed set for specialist and generalist plant species was 19–33% lower at the Restored Fragment. For *B. tubiflora*, there was no significant difference between natural and autonomous seed set within the Restored Fragment or the Nature Reserve Intact (Fig. 3.2a). There was also no significant difference between natural seed set and seed set by pollen supplementation for *B. tubiflora* within any of the study sites, indicating that pollination is optimal at all study sites, including the Restored Fragment. There was a significant interaction between the effect of pollination treatment and site state for both *W. meriana* (p < 0.001; Fig. 3.2b) and *B. orientalis* (p = 0.006; Fig. 3.2c). For *W. meriana*, seed set by pollen supplementations were significantly higher than natural seed set within the Restored Fragment (100%) and the Nature Reserve Fragment (20%), indicating sub-optimal pollination. Natural and autonomous seed set within the Restored Fragment were significantly lower than the Nature Reserve Fragment (86-95%). For *B. orientalis*, seed set produced by pollen supplementations was significantly higher than natural seed set within all sites (94 -99%), indicating sub-optimal pollination, while the species also proved to be incapable of autonomous selfing.

For *F. crispa,* there was a significant interaction between the effect of pollination treatment and site state (p < 0.001). Natural seed set was significantly higher than seed set by pollen supplementations within the Restored Fragment (97%) and within the Nature Reserve Fragment (42%). Autonomous seed set was significantly lower than natural seed set within all sites (97%; Fig. 3.2d). For *M. flaccida*, there was no significant difference between natural seed set and seed set by pollen supplementations, indicating optimal pollination at all sites. Autonomous seed set was significantly lower than natural seed set within all sites (p = 0.01; 36%; Fig. 3.2e). For *O. thyrsoides*, autonomous seed set at all sites was significantly lower than natural seed set (p < 0.001; 95%; Fig. 3.2f). Natural seed set and seed set by pollen supplementation within the Restored Fragment was significantly lower than the Nature Reserve Intact (p < 0.001; 18-26%). There was no significant difference between natural seed set and seed set by pollen supplementation, indicating that pollination of the species is optimal at all sites. While there was no significant difference in seed set between study sites for *T. divaricata,* natural seed set at all sites was significantly higher than seed set by pollen supplementation (p < 0.001; 24%) as well as autonomous selfing *(*p < 0.001; 84%; Fig. 3.2g).

Babiana tubiflora

Watsonia meriana

Brunsvigia orientalis

Pollination treatment
- Autonomous
- Natural
- Pollen supplemented

Ferraria crispa

Moraea flaccida

Ornithogalum thyrsoides
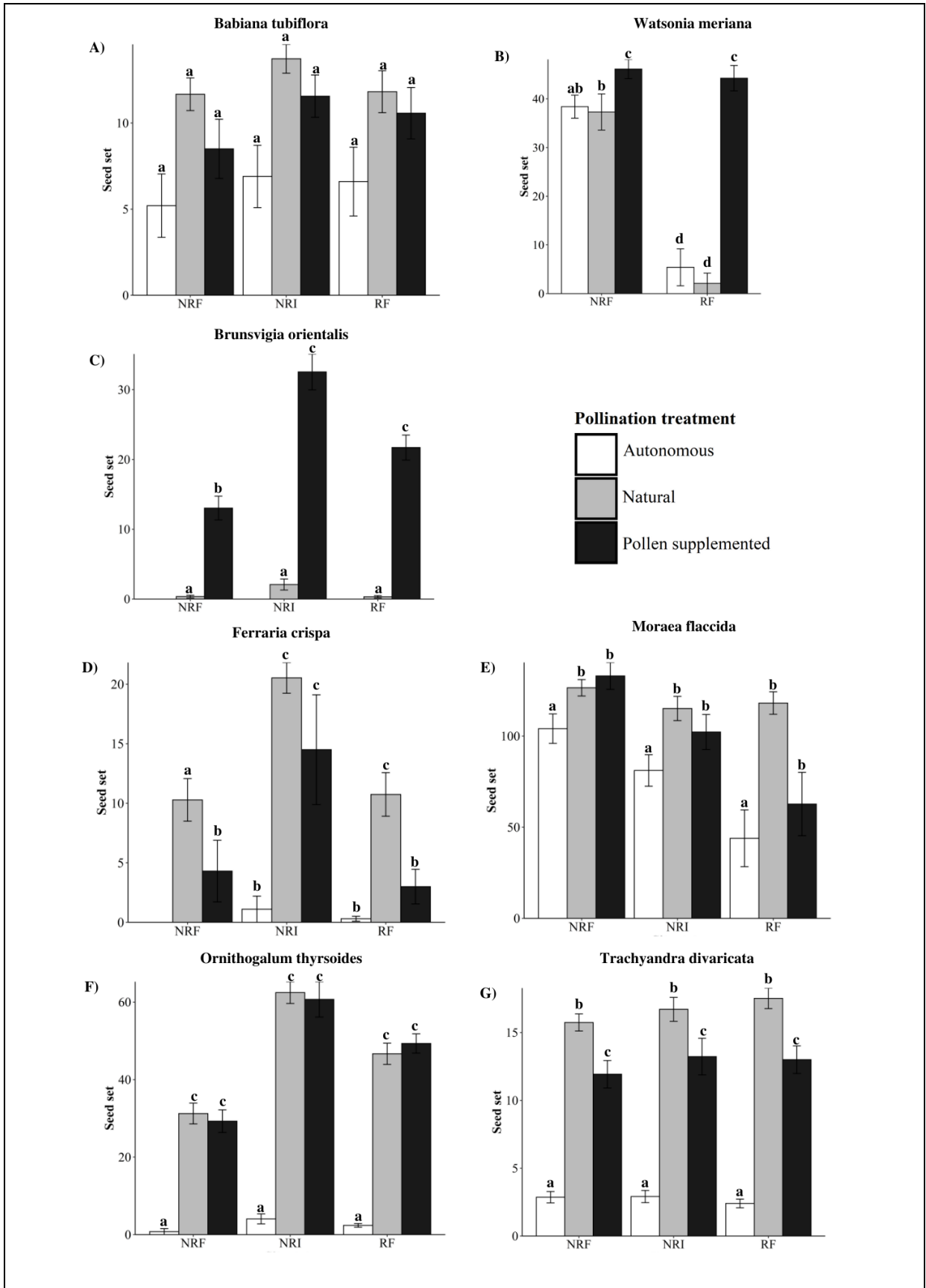
Trachyandra divaricata

Figure 3.2: The seed set of the tested plant species compared within each site. For seed set, flowers/inflorescences which was marked as part of a control group and left open to be naturally pollinated are referred to as "Natural". The seed set of those on which pollen was supplemented by hand are referred to as "Pollen supplemented". Where pollinators were excluded with gauze bags, seed set is referred to as "Autonomous". RF = Restored Fragment NRF = Nature Reserve Fragment NRI = Nature Reserve Intact. The error bars on the graphs indicate one standard deviation of uncertainty while the annotated letters on top of the bars indicate significant differences. A = *Babiana tubiflora*; B = *Watsonia meriana*; C = *Brunsvigia orientalis*; D = *Ferraria crispa*; E = *Moraea flaccida*; F = *Ornithogalum thyrsoides*; G = *Trachyandra divaricata*.

3.5 Discussion

Although my results indicate that pollination may be restored through active vegetation restoration, this may be largely dependent on the choice of plant species used. In terms of specialist plant species, visitation of pollinators was non-existent and subsequently no seed set took place, unless the plant species was capable of autonomous selfing. Because pollinator species richness and visitation rates for two of the four tested generalist plant species were the highest at the Nature Reserve Intact, it may be that connectivity, or an abundance of resources were influencing factors. However according to seed set, these two species were still optimally pollinated at all three study sites. In contrast, the species richness and visitation frequency of pollinators on *Ferraria crispa* was found to be the highest within the restored and fragmented study sites.

The perceived absence of the specialist pollinator of *Babiana tubiflora* as well as the persistence of the plant species at the fragmented study sites, indicates that autonomous selfing seems to be sufficient to replace pollination (Bierzychudek, 1981). This reinforces the theory by Bond (1994), that facultative autonomous selfing may be a compensatory mechanism in certain specialist plants to ensure their survival in the absence of a specialist mutualistic pollinator. Autonomous seed set for the species was variable, but not significantly different to natural seed set at any of the study sites. However, *Brunsvigia orientalis,* showed to be incapable of autonomous selfing and did not receive any pollinator visitors during observations. The species was therefore already absent from small and fragmented sites such as the Restored Fragment and the Nature Reserve Fragment and had to be introduced at these sites for the purpose of the study. Cowling and Bond (1991) found that the numbers of specialist plant species were proportionally low within small and isolated habitat fragments in South African Fynbos. Although they deduced that pollination mutualisms were not affected by fragmentation, data collection for their study was limited to the number of plant species

present at sites and did not include data on pollinator visits or pollen limitation. Even though *B. orientalis* offers nectar resources to *Nectarinia famosa* and *Nectarinia chalybea* in autumn when other sources are scarce (Pauw, 2004), natural seed set was low within the Nature Reserve Intact, with no records of pollination by either of its known pollinators made during observation periods or as ad hoc sightings. This is despite findings by Pauw & Louw (2012), where *N. chalybea* was found throughout urbanized areas. For natural seed set of *B. orientalis* in the Nature Reserve Intact, Pauw (2004) found an average of approximately three to four seeds per capsule, higher than the average of two found in this study. This may be due to a variety of environmental factors during our data collection period (Baskin & Baskin, 2004).

The lower seed set of *Watsonia meriana* for natural pollination in the Restored Fragment could be due to the low density of flowers of the species in this site. A higher natural seed set was recorded in the Nature Reserve Fragment, where there was a high density of flowers of *W. meriana* within a small radius of 50 meters at the site that attracted a *N. famosa* individual observed outside formal observation periods. Plants that are in high density areas are known to receive more pollinator visits than those areas where floral resources are dispersed (Mustajavi et al., 2001; McCallum et al., 2019) even if the population size of the dispersed population is larger (Bernhardt et al., 2008). The effect of fragmentation on specialist pollinators in fragmented habitat depends on the traits these pollinators possess (Larsen et al., 2005). Resource abundance is known to attract nectar feeding birds to an area (Pauw & Johnson, 2017; Geerts et al., 2020). Pauw & Louw (2012) found that *N. famosa* does not advance more than 1km from natural habitat such as conservation areas. It may be that the extent of fragmentation of the Nature Reserve Fragment is not affecting *N. famosa* in the area. The neighbourhood that surrounds the Restored Fragment and Nature Reserve Fragment, has a strict indigenous plant species landscaping policy with regards to private gardens, and public open spaces and plant species with prominent tubular flowers such as *W. meriana* and *Leonotis leonurus* were frequently observed in the area. This may have contributed to providing temporal and spatially favourable nectar sources to *N. famosa* (Colding, 2007; Mnisi et al., 2021), especially during spring when floral resources are most abundant. Where pollinators where excluded, *W. meriana* produced a seed set similar to the natural seed set in the Nature Reserve Fragment which indicates that the species can self-pollinate well, although studies on the closely related *Watsonia knysnana* found that the majority of seeds formed in exclusion experiments were not viable (Bestea et al., 2019). However, the fact that the *W. meriana* had a low natural and autonomous seed set at the Restored Fragment, show that the higher natural seed set at the Nature Reserve Fragment might not necessarily have been due to the presence of *N. famosa,* but rather due to favourable environmental factors (Baskin &

Baskin, 2004). Experimental factors could have played a role, as the specimens in buckets used within the Restored Fragment were sourced from the Nature Reserve Fragment.

The *Ferraria* genus is characterized as a group that has evolved to attract the least typical pollinators of other angiosperm plants, while pollination by flies is specifically important for *F. crispa* (Goldblatt et al., 2009). The high pollinator species richness recorded for *F. crispa* in the Restored Fragment as well as the high visitation frequency of pollinators within the Restored Fragment and the Nature Reserve Fragment may be related to the fact that the study site was significantly close to human dwellings in the form of high-density, suburban apartments, as well as stables housing horses and several other domestic farm animal species. Sarcophagidae and Calliphoridae are known for feeding on decaying animal matter and faeces (Picker et al., 2004), thus the adjacent land-use to the study area could have contributed to attract a large number of Dipteran pollinators. In contrast, Li et al. (2020) found that the density of pollinators where not influenced by the quality of neighbouring habitats, but rather by the quality of the habitat that they occupied. As the Restored Fragment and the Nature Reserve Fragment were recently burnt (respectively 6 months and 6 years prior to the study), this could have contributed to the observed high density of *F. crispa* flowers and consequent higher pollinator visitation rates as opposed to the Nature Reserve Intact where there is no history of fires. Pollination in a newly burnt site can be influenced by the distance to the fire edge, as well as the distance that pollinators are able to travel (Dafni et al., 2012). The short distance between the Restored Fragment and the Nature Reserve Fragment, possibly allowed pollinators to easily reach the post-burn area (Harris & Johnson, 2004). While fire may affect pollination, it is also known to trigger a mass flowering of geophytes in Mediterranean habitats such as South African Fynbos (van Wilgen, 2013).

Pollinators tend to move more frequently between plants in high density areas (Grindeland et al., 2005; McCallum et al., 2019) which would lead to high visitation rates. However, Kaiser-Bunbury et al. (2017), found that pollination restoration depends on the proximity of source populations for pollinators. This corresponds with the pollinator species richness and visitation frequency of pollinators recorded on *Moraea flaccida*, and *Ornithogalum thyrsoides* which was significantly lower at the Restored Fragment than the Nature Reserve Intact, which is in contrast to results found by Forup & Memmott (2005) but corresponds with those of Kaiser-Bunbury (2017). However, it has also been shown that insect species turnover can be high over short spatial scales in the Cape Floristic Region, which suggests that the changes noted in this study may be due to natural variation (Kemp et al., 2017). In terms of connectivity, the species diversity of a site does increase with size, which in effect improves the stability of habitats in the long-term (Garibaldi et al., 2011). The larger the species diversity of pollinator

species are at intact sites, the more effective it can buffer against plant extinctions (Bond, 1994; Ramos-Jilberto et al., 2020).

Regardless, generalist plant species *M. flaccida*, *O. thyrsoides* and *T. divaricata* were still pollinated optimally at the restored and fragmented sites, which corresponds with results found by Forup & Memmott (2005) and Ritchie et al. (2020). Furthermore, the fact that there was no significant difference between seed set, pollinator species richness or visits to *Trachyandra divaricata* between the study sites as well as the high visitation rates of the generalist bee species *Apis mellifera capensis* on all generalist plant species, corresponds with the results of Wenzel et al. (2020) where these pollinators were less affected by urbanization and became dominant in areas that were otherwise species-poor in terms of pollinators. Generalist bees can also compensate for the loss of other pollinator species due to fragmentation and can still be successful pollinators in disturbed habitats (Kearns et al., 1998; Wray & Elle, 2015; Geerts and Pauw 2011).

For generalist plant species *F. crispa* and *T. divaricata*, seed set was lower in pollen supplemented experiments opposed to natural seed set. It may be that floral species undergo protandry (Bawa & Beach, 1981) and that the pollen supplemented clogged an unreceptive stigma and rendered it unreceptive for future natural pollination (King et al., 2013). As all experiments were done in the field, it is highly unlikely that pollen was not viable at the time of supplementation (Stone et al., 1995), although viability could have been reduced if the stigma was unreceptive at first.

While Donaldson et al., 2002 found that seeds of *O. thyrsoides* formed by autonomous selfing had a 78% germination rate, the viability of seeds was not tested in this study for any of the studied plant species, neither did I quantify the pollinator contribution to natural seed set by means of an auto-fertility index (Rodger et al., 2021). Although all generalist plant species formed seeds within exclusion bags, the seed set produced within the bags was significantly lower than natural seed set (Hirayama et al., 2005; Moeller, 2006). The opposite was true for the studied specialist plant species that showed to be capable of autonomous selfing, as there were no significant differences between natural and autonomous seed set. The results have shown that a reintroduction of specialist plant species that are capable of autonomous selfing should either include a high density of floral resources from the start or by allowing the population to grow through autonomous selfing over time to offer enough resources to pollinators. In small urban natures reserves, the latter could potentially also be aided by the presence of nectar-rich neighbourhoods in the surrounding area.

3.6   Conclusion

Successful restoration of pollination showed to be dependent on whether plant species were specialists, generalists or capable of autonomous selfing. The assumption that pollinators will automatically return to an area, once plant species are restored (Devoto et al., 2012), depends on whether the pollinator species are still present in the surrounding landscape (Forup et al., 2008). Once an ecosystem becomes degraded, the specialist pollinators are usually the first to disappear (Dixon, 2009). Restoration practitioners should carefully consider the specific plant species to be reintroduced from an early stage in the planning process (Devoto et al. 2012). While successful cultivation of plant species should be a first consideration, expectations of the probability of the presence and attraction of the pollinators of introduced plant species should be realistic (Menz et al., 2011) and should include considerations on the connectivity of restoration sites. The quality of pollen should be considered, as the lack of receipt of high-quality outcrossed pollen may limit seed set at restored and fragmented sites (Delnevo et al., 2020). To assess pollination in restored sites, monitoring should include data collected before any restoration activities take place, to allow for the ability to evaluate whether vegetation restoration interventions had any impact on pollinators. Planting strategies must be carefully evaluated as pollinator richness is generally known to increase with floral abundance (Ghazoul, 2006). Practitioners should consider whether to include wind or self-pollinated species, which will still reproduce, even when pollinators are scarce (Friedman & Barrett, 2009). In contrast, a "Planting for Pollination" approach could be followed where the choice of plants used in restoration is specifically pursued to attract pollinators (Sabatino et al., 2021; LaBar et al., 2014; Devoto et al., 2012). Molina-Montenegro et al. (2008) describes the "magnet effect", where the inclusion of dominant plant species in restoration lists that are attractive to pollinators, may assist to restore pollinator communities as well as facilitating the pollination of rare plants by supporting a robust and diverse pollinator community (Menz et al., 2011). Overall, the choice of plant species to include in restoration should be based on the characteristics of the restoration site and whether the dispersal and foraging requirements of the targeted pollinators will be met (Cariveau et al., 2020). Furthermore, the effect of fragmentation and patch size on pollinators may vary between taxa as well as restoration contexts (Winfree et al., 2011; Hadley & Betts, 2012; Hadley et al., 2014; Cariveau et al., 2020; Ritchie et al., 2020).

The uncertainty of the viability of seeds that were formed by autonomous selfing necessitates further research to test the germination ability of seeds as well as quantifying the pollinator contribution to natural seed set by means of an auto-fertility index (Rodger et al., 2021). The higher risk of inbreeding associated with autonomous selfing perhaps necessitates that the reliance on this for the survival of restored plant species, should only be used as a last resort

(Igic et al., 2008; Ollerton, 2017). The inclusion of data on pollination webs of restored and fragmented sites should also provide a more comprehensive framework for restoration project planning, as well as the response of generalist and specialist pollinator species to anthropogenic disturbances at the community level. Although the introduction of generalist plants showed to have a greater ability to facilitate ecosystem recovery (LaBar et al., 2014), it is imperative that managers plant with optimal pollination in mind, by also providing sustained floral resources and stepping stone habitats for specialist pollinators in fragmented areas (Sandberg et al., 2016; Wenzel et al., 2020; Mnisi et al., 2021) as those specialist plant species that are incapable of autonomous selfing are otherwise unlikely to survive long-term.

3.7   References

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CHAPTER 4
CONCLUSIONS AND RECOMMENDATIONS

4.1 Summary

Due to the increasing high cost of active restoration programmes (Copeland et al., 2018), managers need to utilize only the most cost-effective methods to apply available resources as efficiently as possible (Kimball et al., 2015). The need for landscape scale restoration is becoming increasingly important as we enter the UN Decade on Ecosystem Restoration. Hence, the need for active restoration costs that do not increase in a linear manner as restoration areas are expanding is greater than ever.

Active restoration usually entails the removal of disturbances and consequent remedial action through revegetation (Palma & Laurance, 2015). Specifically, frequently used techniques used for active restoration of Mediterranean-type biomes are prescribed burning and sowing (Bond & Keeley, 2005; Nevill et al., 2018). Fire is an important ecological driving force in Mediterranean biomes (Keeley, 2012) including South African fynbos which is both dependent on and adapted to frequent fires (van Wilgen, 2009). My findings in chapter 2 suggest that fire remains one of the most cost-effective options for restoration in Mediterranean-type systems, especially when scaling up active restoration. Other than topsoil translocation, fire combined with sowing and planting was the most successful treatment at a reasonable cost, despite planting being expensive. My results also demonstrate that the number of factors included in a restoration treatment corresponds positively with the cost, but that the most successful treatment is not necessarily the most expensive option.

While sowing is a treatment that can effectively be scaled up to use on larger areas (Hall et al., 2021), the success of the method is dependent on whether the appropriate germination cues of species have been achieved (Hall et al., 2021) and if the native species sown will be able to out-compete a possible secondary invasion of alien species (Nsikani et al., 2020). The stoloniferous invasive alien grass species that threaten South African Fynbos, especially in urban areas, remain expensive to remove mechanically. If the use of large machinery is unsuitable for the area, other methods should be explored for the control of these grass species in shrubland restoration sites such as South African Fynbos.

According to my results, the synergistic effect of a prescribed burn, followed by planting, can greatly improve the success of restoration attempts in terms of survival of the introduced plant species, as well as restoring native shrub cover. The planting of propagated plant species is used far less than sowing, possibly due to the high costs and difficulty to upscale the treatment (Holmes, 2008). However, the possibility of using planting on a larger scale whilst still being

cost-effective may be possible through applied nucleation (Corbin & Holl, 2012). Although the method has been researched within forest ecosystems, no clear methodology has yet been established for Mediterranean shrublands while data for Fynbos is based on preliminary work (Holmes et al., 2022).

The Cape Fynbos of the Cape Floristic Region of South Africa has high levels of biodiversity and endemism (Rebelo et al., 2006), which often leads to limited technical knowledge of cultivating plants for restoration (Fowler et al., 2015). This problem may be overcome by using topsoil translocation as an active restoration method (Fowler et al., 2015). In this thesis I show that, in unique cases, where topsoil can be translocated from intact areas, the method can be successful and cost-effective – if combined with planting. However, topsoil translocation cannot be seen as mitigation for the loss of endangered habitat (Bulot et al., 2014) and will certainly not successfully replicate a lost habitat; it would rather create a habitat that resembles the one that was lost (Bullock, 1998). Topsoil translocation could be a viable solution for conserving native habitat which is located in areas where development is unavoidable or where the integrity of small and fragmented sites is compromised.

In urban environments conservation areas are often small and fragmented, which is associated with degradation and consequent loss of stability (Garibaldi et al., 2011). This is usually due to a loss of connectivity as well as a myriad of negative edge effects from the urban edge (Rebelo et al., 2011). Cowling & Bond (1991) found that the minimum size needed for natural fragments of lowland Fynbos to avoid species losses is 4–15ha. Due to long-term environmental fluctuations and the fact that the viability of plant populations can diminish when the minimum viable population sizes of species are not present, it is inevitable that certain plant species and other ecological functions such as pollination at small, fragmented natural sites will not survive in the long-term without intensive management and restoration (Godefroid et al., 2011).

It is important for restoration ecologists to factor in pollination when planning projects and when choosing plants species to reintroduce (Dixon, 2009; Martins & Antonini, 2016). Examples of factors that could affect the choice of plant species are those of "framework" and "bridging species" (Menz et al., 2011) or specialist and generalist pollinators (Ollerton, 2017; Pauw & Stanway, 2014), as well as whether plants are dependent on an external vector for pollination to take place, or self-pollination. For example, flowering in Mediterranean woody resprouters is usually delayed to later successional stages after a fire (Keeley, 2012) - therefore, pollinators will not be able to utilize these species during the early post-fire stages (Dafni et al., 2012) and will need alternative floral resources during this time. Pollination networks may be successfully restored in degraded areas by acknowledging the ecological

requirements of pollinators, as well as the type of plant species that attract and sustain key pollinator species (Menz et al., 2011).

The number and variety of plants species that are reintroduced for active restoration are often limited (Meli et al., 2014) due to limited funds and resources (De Groot et al., 2013). However, this could also be due to practical reasons, in that some species are simply more difficult to cultivate and essentially restore than others. While specialist plant species may be sought after to reintroduce into restoration sites, limited numbers of seeds are often available at small and fragmented sites due to pollinators already being either absent or scarce (Geerts & Pauw, 2012). The problem of pollen limitation of these specialist plants may then persist within small newly restored populations and may be exacerbated further if restoration sites are in highly fragmented areas (Hadley & Betts, 2012). My results in Chapter 3 indicates that the interaction of pollination syndrome and autonomous selfing are important requirements for pollination and subsequent seed set of specialist plant species in urban fragments. The choice of plant species to be included in restoration plans should be determined according to which plant species play an important ecological role by being attractive to pollinators (Menz et al., 2011). By knowing the ecological requirements of pollinators, especially those specialist pollinators that are easily affected by habitat degradation and fragmentation, the unnecessary wastage of limited time and resources that is spent on restoring "living-dead" specialist plant species that will disappear over time due to pollen limitation, can be prevented. This Field of Dream hypothesis ("if you build it, they will come") (Palmer et al., 1997), often fails due to a lack of requirements needed by pollinators for survival (de Araújo et al., 2018), specifically when including specialist plant species in restoration plans.

A wide variety of pollinators will increase stability and colonization rates of newly established plant communities (Garibaldi et al., 2011; Cusser et al., 2013; Cariveau et al., 2020). Careful consideration should be taken, while keeping in mind which pollinators plant species will attract and if those pollinators will be able to reach the restoration site (Menz et al. 2011). It is considerations like these that should form important guidelines when planning vegetation restoration. My results show that generalist plant species have a greater potential to facilitate ecosystem recovery in terms of pollination. Even though connectivity proved to be an important requirement in terms of pollinator species richness and visitation rates for two of the four tested generalist plant species, the same two generalist plant species were optimally pollinated at the restoration site in terms of seed set. However, providing sustained nectar sources, floral abundance and stepping-stones for specialist pollinators such as birds in South African Fynbos, is important to maintain the presence of specialist plant species that contribute to habitat integrity, especially within isolated urban sites (van Zyl & Taylor, 2021).

The inclusion of the correct choice of plant species in restoration projects (for example wind or self-pollinated species) may potentially increase the long-term success rates of very costly restoration projects as these plants may still survive, even when pollinators are scarce (Friedman & Barrett, 2009). In contrast, a "Planting for Pollination" approach could be followed where the choice of plants used in restoration is specifically pursued to attract pollinators (Sabatino et al., 2021; LaBar et al., 2014; Devoto et al., 2012). This should include consideration of the characteristics of the restoration site and whether the dispersal and foraging requirements of the targeted pollinators will be met (Cariveau et al., 2020).

4.2 Implications of thesis results

This study shows that a combined approach of cost-effective vegetation restoration ecology and pollination biology, with a plant species-specific approach to accommodate generalist, as well as specialist pollinator species, should be used when planning active restoration. When restoration takes place, it needs to be considered whether the mutualistic partnerships between plants and pollinators will also be restored. If not, the high costs involved in restoration projects will go to waste. This is due to the viability of plant populations which can diminish when the minimum viable population sizes of plant species are not present and the fact that certain plant and pollinator species at small, fragmented natural sites may not survive in the long-term without ongoing and intensive management (Godefroid et al., 2011).

4.3 Recommendations

Sowing as a restoration treatment proved unsuccessful within this study. A better understanding is needed of seedling biology and of the germination cues needed for successful recruitment of species. In terms of cost, a clear methodology needs to be developed for the use of applied nucleation of propagated plants within Mediterranean biomes such as Fynbos. I carried out restoration treatments with methods that were suited to a small-scale urban restoration project. In larger areas, mechanised options could be used which could be less labour-intensive. Future studies should aim to incorporate long-term data collection, as two years is a relatively short time to assess the survival of introduced plant species and ecological functions such as pollination (Holmes et al., 2020). The inclusion of data on pollination webs of restored and fragmented sites opposed to intact natural sites should also provide a more comprehensive framework for restoration project planning, as well as the response of generalist and specialist pollinator species to anthropogenic disturbances, specifically on a community level in critically endangered Cape Flats Sand Fynbos.

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APPENDIX A: The cost of each restoration treatment factor for the actual area size treated, as well as the cost scaled to 1 ha.

Treatment factors	Hectares treated	Cost (ZAR)	Cost/ha (ZAR)
Burn	2	R36,381	R36,381
Sow	0.12	R10,415	R86,792
Plant	0.16	R17,760	R111,000
Mulch	0.56	R13,614	R24,311
Soil	1.12	R47,705	R42,594
Remove-grass	0.03	R6,750	R225,000

SUPPLEMENTARY MATERIAL

Table S1. The effect of restoration treatment, years after treatment, and their interaction on native species richness.

Factor	Estimate	SE	z value	Pr(>|z|)	95% CI
Burn	-0.31178	0.10277	-3.03	0.002415	-0.513 to -0.11
Burn-sow	-0.31178	0.10277	-3.03	0.002415	-0.513 to -0.11
Burn-sow-plant	0.04368	0.09348	0.47	0.640334	-0.140 to 0.227
Soil-plant	-0.08377	0.09653	-0.87	0.385513	-0.273 to 0.105
Soil-mulch-sow-plant	-0.11333	0.09728	-1.16	0.244052	-0.304 to 0.077
Remove-grass-sow-plant	-0.40770	0.10572	-3.86	0.000115	-0.615 to -0.2

Table S2. The effect of restoration treatment, years after treatment, and their interaction on alien species richness.

Factor	Estimate	SE	z value	Pr(>|z|)	95% CI
Year	-0.23622	0.08663	-2.73	0.0064	-0.406 to -0.066

Table S3. The total number of alien plant species present within each restoration treatment during the first and the second year.

Restoration treatment	Year 1	Year 2
Burn	12	11
Burn-sow	11	9
Burn-sow-plant	12	10
Reference site	15	15
Remove-grass-sow-plant	14	13
Soil-mulch-sow-plant	17	12
Soil-plant	15	15

Table S4. The effect of the different restoration treatments on native species' growth form richness (number of shrub, forb and graminoid species).

Factor	Estimate	SE	z value	Pr(>|z|)	95% CI
Burn	-0.301867	0.128709	-2.345	0.019010	-0.554 to -0.05
Burn-sow	-0.301867	0.128709	-2.345	0.019010	-0.554 to -0.05
Burn-sow-plant	-0.246297	0.126694	-1.944	0.051891	-0.495 to 0.002
Remove-grass-sow-plant	-0.808373	0.155832	-5.187	2.13e-07	-1.114 to -0.503
Soil-mulch-sow-plant	-0.350657	0.130546	-2.686	0.007230	-0.607 to -0.0948
Soil-plant	-0.456017	0.134734	-3.385	0.000713	-0.72 to -0.192

Table S5. The effect of restoration treatment during Year 1 and Year 2 on planted species survival (Fig. 2.4a).

Factor	Estimate	SE	z value	Pr(>|z|)	95% CI
Year 1					
Remove-grass-sow-plant	-0.04447	0.60601	-0.073	0.941507	-1.232 to 1.143
Soil-mulch-sow-plant	-0.39791	0.60050	-0.663	0.507572	-1.575 to 0.78
Soil-plant	-0.03173	0.60320	-0.053	0.958045	-1.214 to 1.151
Year 2					
Remove-grass-sow-plant	-2.10876	0.56168	-3.754	0.000174	-3.209 to -1.008
Soil-mulch-sow-plant	-1.64754	0.55247	-2.982	0.002863	-2.730 to -0.565
Soil-plant	-1.88645	0.55864	-3.377	0.000733	-2.981 to -0.792

Table S6. The effect of restoration treatment, years after treatment, and their interaction on sowed species survival.

Factor	Estimate	SE	z value	Pr(>|z|)	95% CI
Burn-sow-plant	0.26497	0.19055	1.391	0.164374	-0.109 to 0.638
Remove-grass-sow-plant	-0.19000	0.20019	-0.949	0.342576	-0.582 to 0.202
Soil-mulch-sow-plant	0.45137	0.18841	2.396	0.016588	0.082 to 0.82

Table S7: Pollinators that were observed at each study site. Pollinator species were either identified from photographs or caught specimens. Identifications were done at least up to family level, and where possible up to species level. RF = Restored Fragment NRF = Nature Reserve Fragment NRI = Nature Reserve Intact.

Plant species	Site	Pollinator family / genus / species
F. crispa	RF	*Apis mellifera capensis*; Calliphoridae sp. 1; Calliphoridae sp. 2; Empididae; Sarcophagidae sp.1; Sarcophagidae sp. 2; *Scathophaga stercoraria;* Scathophagidae sp. 2; Syrphidae
F. crispa	NRF	*Apis mellifera capensis*; Calliphoridae sp. 1; Calliphoridae sp. 2; Sarcophagidae sp. 2; *Scathophaga stercoraria;* Scathophagidae sp. 2
F. crispa	NRI	*Apis mellifera capensis*; Calliphoridae sp. 1; Calliphoridae sp. 2; Sarcophagidae sp.1; Sarcophagidae sp. 2; *Scathophaga stercoraria;* Scathophagidae sp. 2; Syrphidae
M. flaccida	RF	-
M. flaccida	NRF	*Apis mellifera capensis*
M. flaccida	NRI	*Apis mellifera capensis*; *Monolepta bioculata;* Halictidae*;* Syrphidae
O. thyrsoides	RF	Apidae sp. 2; *Heterochelus* sp.
O. thyrsoides	NRF	*Apis mellifera capensis*; Apidae sp. 2; Calliphoridae sp. 1
O. thyrsoides	NRI	*Apis mellifera capensis*; Apidae sp. 2; *Amata cerbera;* Eristalinae; Halictidae; Sarcophagidae sp. 2
T. divaricata	RF	*Apis mellifera capensis*; Apidae sp. 2
T. divaricata	NRF	*Apis mellifera capensis*; Syrphidae;
T. divaricata	NRI	*Apis mellifera capensis*; Apidae sp. 2; Calliphoridae sp. 1; Halictidae
B. tubiflora	RF	-
B. tubiflora	NRF	-
B. tubiflora	NRI	-
W. meriana	RF	-
W. meriana	NRF	-
W. meriana	NRI	-
B. orientalis	RF	-
B. orientalis	NRF	-
B. orientalis	NRI	-

Table S8: The effect of floral neighbourhood on the visitation rate of pollinators. This had no significant effect and was therefore excluded from further analyses.

Factor	Estimate	SE	t value	Pr(>|z|)
Floral neighbourhood	-0.005690	0.004428	-1.285	0.2

Table S9: The average pollinator visitation frequency of the observed functional groups per plant species at each site.

Plant species	Specialization	Site	Functional groups	Visitation frequency
F. crispa	Generalist	Restored Fragment	Long-tongue bees	3.1 (±4.6)
F. crispa	Generalist	Restored Fragment	Flies	0.1 (±0.3)
F. crispa	Generalist	Restored Fragment	Carrion flies	15.6 (±15.4)
F. crispa	Generalist	Nature Reserve Fragment	Long-tongue bees	1 (±2.9)
F. crispa	Generalist	Nature Reserve Fragment	Carrion flies	32.5 (±18.3)
F. crispa	Generalist	Nature Reserve Intact	Long-tongue bees	0.5 (±0.9)
F. crispa	Generalist	Nature Reserve Intact	Flies	0.2 (±0.5)
F. crispa	Generalist	Nature Reserve Intact	Carrion flies	8.9 (±12.9)
M. flaccida	Generalist	Nature Reserve Fragment	Long-tongue bees	0.2 (±0.6)
M. flaccida	Generalist	Nature Reserve Intact	Long-tongue bees	0.5 (±0.8)
M. flaccida	Generalist	Nature Reserve Intact	Short-tongue bees	0.7 (±1)
M. flaccida	Generalist	Nature Reserve Intact	Flies	0.2 (±0.4)
M. flaccida	Generalist	Nature Reserve Intact	Beetles	0.3 (±0.5)
O. thyrsoides	Generalist	Restored Fragment	Long-tongue bees	0.09 (±0.2)
O. thyrsoides	Generalist	Restored Fragment	Beetles	0.007 (±0.01)
O. thyrsoides	Generalist	Nature Reserve Fragment	Long-tongue bees	1.2 (±0.9)
O. thyrsoides	Generalist	Nature Reserve Fragment	Carrion flies	0.009 (±0.02)
O. thyrsoides	Generalist	Nature Reserve Intact	Long-tongue bees	1 (±1)
O. thyrsoides	Generalist	Nature Reserve Intact	Short-tongue bees	0.01 (±0.03)
O. thyrsoides	Generalist	Nature Reserve Intact	Settling moth	0.2 (±0.3)
O. thyrsoides	Generalist	Nature Reserve Intact	Flies	0.03 (±0.05)
O. thyrsoides	Generalist	Nature Reserve Intact	Carrion flies	0.03 (±0.06)
T. divaricata	Generalist	Restored Fragment	Long-tongue bees	14 (±8.1)
T. divaricata	Generalist	Nature Reserve Fragment	Long-tongue bees	8 (±7)
T. divaricata	Generalist	Nature Reserve Fragment	Flies	0.7 (±1.5)
T. divaricata	Generalist	Nature Reserve Intact	Long-tongue bees	4.4 (±3.3)
T. divaricata	Generalist	Nature Reserve Intact	Short-tongue bees	0.6 (±0.9)
T. divaricata	Generalist	Nature Reserve Intact	Carrion flies	0.08 (±0.2)
B. tubiflora	Specialist	Restored Fragment	-	-
B. tubiflora	Specialist	Nature Reserve Fragment	-	-
B. tubiflora	Specialist	Nature Reserve Intact	-	-
W. meriana	Specialist	Restored Fragment	-	-
W. meriana	Specialist	Nature Reserve Fragment	-	-
W. meriana	Specialist	Nature Reserve Intact	-	-
B. orientalis	Specialist	Restored Fragment	-	-
B. orientalis	Specialist	Nature Reserve Fragment	-	-
B. orientalis	Specialist	Nature Reserve Intact	-	-