INVASION OF ALIEN SPECIES ON ROBBEN ISLAND: CAUSES AND IMPACTS ON PHYLOGENETIC DIVERSITY OF NATIVE PLANT COMMUNITIES

by

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DECLARATION

I declare that this dissertation hereby submitted to the University of Johannesburg for the degree MAGISTER SCIENTIAE (Botany) has not been previously submitted by me for the degree at this or any other University, that it is my work in design and execution, and that everybody who contributed and all materials contained therein has been duly acknowledged.

Signed: Bezeng Simeon Bezeng

Date: 07 February 2012

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ABSTRACT

Invasive species are a considerable threat to ecosystems globally, especially on islands where species diversity can be relatively low. Understanding the drivers of invasion is the first step towards an adequate management plan. Although Darwin's naturalisation hypothesis has fuelled our understanding in this regard, several studies provided mixed results, suggesting that invasion success might be context-dependent. The main objectives of this study are two-fold: (1) testing Darwin hypothesis on Robben Island, and (2) investigating the relative role of invasive alien plants on phylogenetic diversity (PD) loss in native community. I sampled extensively the flora of the island, and using a Bayesian analysis, I reconstructed its phylogeny based on two plastid DNA loci, *rbcLa* and *matK*. I also surveyed a total of 127 plots of 50 x 50 m (i.e. local communities) where species presence/absence was recorded. Analysing phylogenetic patterns of the native and invasive floras at both regional (phylogeny level) and smaller scales (plots level), I found that invasive species are, on average, more distantly related to the native communities, giving strong support to the hypothesis tested. Furthermore I found that native communities have accumulated lower PD than alien communities; and that local communities are more overdispersed than expected. These findings suggest that competitive interactions might be the major ecological forces shaping plant communities, with the possibility of alien being higher competitors than native, and therefore decreasing native plant diversity. The implications of these findings for the recovery of native plants are also discussed.

Key words: Invasion biology - Darwin’s naturalisation hypothesis - Phylogenetic diversity - Community structure - Conservation - Robben Island, South Africa.

TABLE OF CONTENTS

Acknowledgements-- iii

Abstract-- v

CHAPTER ONE

GENERAL INTRODUCTION

1.1. Invasion concept-- 1

1.2. Invasion impacts from ecological and economical perspectives------- 2

1.3. Understanding drivers of invasion success--------------------------------- 4

1.3.1. Species ecological parameters-- 4

1.3.2. Habitat characteristics-- 5

1.3.3. Phylogenetic approach--- 5

1.4. Invasion success and biodiversity loss: implication for invasion management-- 6

1.5. Objectives of the study-- 7

1.6. Outline of the dissertation-- 8

CHAPTER TWO

A phylogenetic approach towards understanding the drivers of plant invasiveness on Robben Island, South Africa

2.1. Introduction --- 10

2.2. Study site-- 12

2.3. Materials and Methods -- 17

2.3.1. Botanical inventory and sampling-- 17

2.3.2. Phylogeny reconstruction-- 49

2.3.3. Data analyses--- 50

2.4. Results-- 51

2.5. Discussion--- 61

CHAPTER THREE

ALIEN INVASIVE PLANTS ARE ‘BACK-SEAT DRIVERS’ OF LOSS IN PHYLOGENETIC DIEVRSITY IN NATIVE COMMUNITIES ON ROBBEN ISLAND

3.1. Introduction--- 67
3.2. Materials and methods-- 69
3.2.1. Community sampling-- 69
3.2.2. Data analysis--- 69
3.3. Results--- 71
3.3.1. Diversity on the Island-- 71
3.3.2. Community structure on the Island--------------------------------------- 71
3.3.3. Phylogenetic beta diversity on the island-------------------------------- 72
3.3.4. Comparison of PD observed versus PD expected-------------------- 77
3.4. Discussion-- 83
3.5. Conclusion-- 85

CHAPTER 4

GENERAL CONCLUSION--- 87

CHAPTER 5

REFERENCES-- 91

LIST OF FIGURES

CHAPTER 1

CHAPTER 2

Figure 2.1. Map indicating the position of Robben Island relative to mainland and West Coast Strandveld vegetation (indicated with white arrow)---12

Figure 2.2. Robben Island is an important habitat for avifauna---------13

Figure 2.3. Human induced disturbances to the natural vegetation on the Robben Island. A: Lime quarry; B: Stone quarry; C: Airstrip; and D: Remains of army base---14

Figure 2.4. Comparison of Robben Island at two different periods---15

Figure 2.5. Some areas on the island are covered with huge invasions of A: *Acacia cyclops* and B: *Eucalyptus* species----------------------------16

Figure 2.6. Examples of native species found on the island--------------17

Figure 2.7. Some invasive species found on the island--------------------18

Figure 2.8. DNA sequences, collection data and pictures available on BOLD for the invasive species, (here *Acacia cyclops* is showed)--------19

Figure 2.9. Map indicating the random distribution of plots on the island (in brown). Shaded areas (in red) specify buildings and gardens--------48

Figure 2.10. Phylogenetic tree of the flora of Robben Island, except *Amborella trichopoda*, which is used as outgroup----------------------------52

Figure 2.11. Chronogram with scale indicating node ages (in million years) at the bottom and blue bars representing 95% confidence intervals for node ages--55

Figure 2.12. Boxplots of phylogenetic nearest neighbor distances (PNND), at island scale, PNND at plot scale and mean phylogenetic distance (MPD), in million years on Robben Island for each pair of native-invasive (Nat_Inv) plants compared to each native-native (Nat_Nat) pair and invasive-invasive (Inv_Inv) pair-------------------------57

Figure 2.13. Bootstrapping analysis to demonstrate the effect of Chance on the longer distances between Invasives and Natives--------59

Figure 2.14. The effect of scale dependency at both small and large scales on the longer distances between natives and invasive------------60

CHAPTER 3

Figure 3.1. Phylo-ordination of plant communities on Robben Island--73

LIST OF TABLES

CHAPTER 1

CHAPTER 2

Table 2.1. List of taxa with voucher information and GenBank accession numbers for each DNA region. ----------------------------------21

Table 2.2. Inventory of all plants recorded on Robben Island (2010 & 2011)--30

Table 2.3. Two-way Anova showing the effect of scale on the longer distances between natives and invasive-------------------------------------60

CHAPTER 3

Table 3.1. Pattern of diversity and community metrics on Robben Island--74

Table 3.2. Comparison of observed PD vs. expected--------------------78

CHAPTER 1

GENERAL INTRODUCTION

1.1. Invasion concept

Invasive species are species that are introduced to a new environment outside their native distribution range where they become not only naturalised but also colonisers (Lockwood et al. 2007). Their naturalisation is likely favoured by local biotic and abiotic conditions to which they were probably pre-adapted (Pulliam 2000; Soberón & Peterson 2005). Several traits have been identified as driving successful invasion: effective reproductive and dispersal mechanisms, high competitive ability, release from natural enemies, and ability to occupy “empty niches” (Elton 1958; Baker 1974; Bazzaz 1986; Blossey & Notzold 1995; Daehler 2001).

However, invasion success is primarily a result of ecosystem disruption usually driven by human activities (Groves & Di Castri 1996). With the current rise in globalisation, transport modes have undergone a faster development, which has intensified the introduction of biological materials (e.g. plants) into new and remote areas. Many of these plants become established, and spread beyond their native range to suitable habitats (Mack et al. 2000). The transport of these materials beyond their native range can be intentional or accidental. Intentionally, plant materials are introduced outside their native range to serve as crop plants, timber and firewood, ornamentals and garden plants, biological control agents, or to stabilise sand dunes thereby preventing soil erosion (van Wilgen et al*.* 2001). Accidental introduction occurs through various means like vessels, air or overland. Although accidental introduction also has detrimental impacts, most of the reported negative impacts result from intentional introduction, following escape from gardens, agricultural lands or from forests (Mack et al. 2000; Lambdon & Hulme 2006).

Nevertheless, not all of these biological materials carried around the world succeed to establish in new environments or become pests, although they may change the native species composition in one-way or the other (Mack et al. 2000). The globalisation process is gaining grounds each year, and is likely to continuously reshape the flora of native species.

1.2. Invasion impacts from ecological and economical perspectives

Human-induced invasion processes are usually more dynamic, quick, and dramatic than accidentally induced processes (Lockwood et al. 2007). The extant of their ecological and economic impacts make them a central issue in ecology and conservation biology (Bergmans & Blom 2001). These impacts raise serious concern among ecologists; conservationists and land managers, primarily due to the alteration of agricultural systems, waterways, land cover change, and local biodiversity. Invasive plant species have significantly threatened biodiversity globally with huge ecological and economic impacts especially at small scale such as islands (Pyšek 1995; Williamson 1996; Mack et al. 2000; Pimentel et al. 2000). The susceptibility of islands to plant invasion has been attributed to the presence of unsaturated communities, and poor competitive ability of native species when faced with invasive species (Carlquist 1965; Hulme 2004)

At ecological scale, plant invaders have greatly altered ecosystem functioning by disrupting native species composition and structure (Mack et al. 2000; Rice & Emery 2003). Such alterations lead to loss of biodiversity and ecosystem services (e.g. freshwater, pollination etc.), agricultural productivity and even human health (van Wilgen et al. 1998; Winter et al. 2009). From a community or ecosystem perspective, the largest ecological problem caused by invasive plants is the disruption of entire ecosystem services (D'Antonio & Vitousek 1992; van Wilgen et al. 1996; Schmitz et al. 1997). However, governments and public at large are still reluctant to provide support for the prevention and control of invasive plants, maybe due to a lack of understanding of the link between nature and economy (Mack et al. 2000).

From economical perspective, ecosystem disruption due to invasives may lead to a loss in potential economic output i.e. reduced crop production, fisheries, forestry and animal farming (U.S. Congress 1993). Similarly, the eradication of invasives with the final objective of recovering native flora is money-consuming (Pimentel et al. 2000). Though difficult to quantify loss of biodiversity in terms of monetary value, Pimentel et al. (2000) attempted to tabulate the annual cost of invasive species in the United States (US). This study reveals that the US loss about $137 billion per year due to invasive plant species. In Africa, limited studies have been conducted to quantify cost of invasive plants species. However, studies in South Africa for example provide important insights: (1) the effect of invasive plants on the fynbos ecosystem is estimated at over $11.75 billion (Higgins et al. 1997; van Wilgen et al. 2001); (2) the total cost of lost water resources due to invasion would be about $3.2 billion on the Agulhas Plain alone (Turpie & Heydenrych 2000); (3)

the net present cost of invasion by black wattles amounts to $1.4 billion (van Wilgen et al. 2001); and (4) the cost to eradicate alien plant invasions in South Africa is around $60 million per year for an estimated 20 years (Versfeld et al. 1998). These alarming statistics have led the South African Government to establish the 'Working for Water' programme with the specific objective of controlling and monitoring invasive alien plants to protect water resources and ensure the security of water supply (Le Maitre et al. 1996; van Wilgen et al. 1996; 1997; 1998). The South African government has spent over $100 million on this programme between 1995 and 2000. Such economic expenditures are ill afforded on the African continent where basic health, education, and agricultural services are still poorly delivered.

1.3. Understanding drivers of invasion success

Attempts to understand the major drivers of invasion success have stemmed from three areas of interest.

1.3.1. Species ecological parameters

The use of ecological traits such as testing whether certain life history traits are correlated with invasion success is broadly developed to study invasion biology (Rejmanek & Richardson 1996; Hayes & Barry 2008). Numerous species traits have been identified as useful predictors of invasiveness, such as habit (Gleason & Cronquist 1991), seed weight (Flynn et al. 2006), leaf mass per area (Reich et al. 2007), etc. For example, Richardson & Bond (1991) were able to show how some characteristics of pine species in South Africa can be used to explain their invasion success. However, the predictive power of life history traits is mixed and limited (Mack 2003), and in most cases, is only useful within closely related groups (Rejmanek & Richardson 1996; Holm et al. 1997).

1.3.2. Habitat characteristics

Several studies also used an approach that involved testing whether communities that are frequently invaded possess specific characteristics that underlie their susceptibility to invasion (e.g. Elton 1958; Naeem et al. 2000). One of the major characteristics of habitat that could favour its invasion is linked to absence of natural enemies. Indeed, a release from natural enemies (regulate the population of their preys – here introduced species) is more likely to cause the population of introduced species to explode (Elton 1958; Blossey & Notzold 1995).

Although this approach has provided useful insights, it may prove difficult, mainly when some key ecological abilities of introduced species are lacking (Mack et al. 2000).

1.3.3. Phylogenetic approach

The use of phylogenetic information to explain invasion success has dominated recent studies (e.g. Proches et al. 2008; Winter et al. 2009; Cadotte et al. 2009; Schaefer et al. 2011). The rationale of this approach, known as Darwin naturalisation hypothesis is, species that are distantly related to native species should stand a greater chance of being successfully established in new environments (Darwin 1859). Darwin, in his hypothesis assumed that closely related plants would be highly competing for resources in the same habitat than distantly related species, resulting in the exclusion of many species i.e. low competitors.

Attempts to test this hypothesis provided mixed results. While some studies found Darwin's theory applicable for invasion management (e.g. Strauss et al*.* 2006; Schaefer et al*.* 2011), others challenge its universality (e.g. Cahill et al*.* 2008; Diez et al. 2008). The applicability of Darwin's naturalisation hypothesis to invasion management may therefore be context (or scale) dependent; it is critical therefore to evaluate the hypothesis within the appropriate context. In this thesis, I use a phylogenetic approach to understand what drives plant invasion on the Robben Island in South Africa, and define the consequences of invasion on native plant diversity.

1.4. Invasion success and biodiversity loss: implication for invasion management

Invasive species have long been assumed to be the sole cause of native species decline and also changing ecosystem functioning (Davis 2003; Gurevitch & Padilla 2004; Sax & Gaines 2008). Recent studies show that such conclusion should be drawn with caution, as invasives could only be the secondary drivers of species loss (Bauer 2012). Three scenarios are expected depending on the relative roles of invasives in ecosystem alteration and land cover change: Invasives could be regarded as 'passengers', 'back-seating drivers', or 'drivers' of change (Bauer 2012).

In the 'passenger' model, invasives are regarded as a symptom of native species decline, but not the primary cause of ecosystem disruption and diversity loss in native communities. However, in the 'back-seat' model, invasion success of exotic species is the consequence (not the primary cause) of ecosystem being already disturbed by other factors (e.g. human activities). The occurrence of disturbance may stress native species, leading to population decline; and exotics just benefit from the change in disturbance regime to further the loss of native species (Bauer 2012). Therefore, exotic effect on ecosystem is indirect. In contrast, under the ‘driver model’, invasives are the direct cause of biodiversity loss and ecosystem disruption.

Investigating the models of invasion success has implications for the management of invasive species as it provides a basis to understand and predict the response of native species to invasive species. For example, if invasives are passengers of back-seat drivers of biodiversity loss, invasion management should essentially focus on finding out what is the primary cause. In such scenario, the removal of invasives alone would be completely inefficient. In contrast, such precaution is likely to lead to the recovery of native community, only if invasives are drivers, i.e. direct cause of ecosystem disruption (Bauer 2012).

1.5. Objectives of the study

The main objective of the study is to understand what drives plant invasiveness on Robben Island. Specifically, I intend to:

- Generate a DNA database (DNA barcode) for the flora of the island;
- Reconstruct the phylogeny of all plants on the island using the two barcoding genes, *rbcLa* and *matK*;
- Test Darwin’s Naturalisation hypothesis; and
- Assess the effect of invasive alien species on phylogenetic diversity on the native flora on the island.

1.6. Outline of the dissertation

This dissertation comprises four chapters outlined as follows:

- **Chapter One: General introduction**

Here I present a general overview of plant invasion, its consequences and approaches to study plant invasion.

- **Chapter Two: A phylogenetic approach towards understanding the drivers of plant invasiveness on Robben Island, South Africa**

In this chapter, I used a phylogenetic approach to test Darwin's naturalisation hypothesis on Robben Island. I reconstructed a phylogeny of all native and non-native plants (regional pool) on the island and used this phylogeny to investigate Darwin's hypothesis.

- **Chapter Three: Alien invasive plants are 'back-seat drivers' of loss of phylogenetic diversity in native communities on Robben Island**

Here, I seek to understand what is the primary cause of phylogenetic diversity loss in native species and how the various communities are dispersed across a series of plots laid out on the island.

- **Chapter Four: General conclusions and recommendations.**

Finally, I present a brief summary of my findings and the implications for the current conservation programme to rehabilitate the native diversity on the island.

CHAPTER TWO

A Phylogenetic Approach Towards Understanding the Drivers of Plant Invasiveness on Robben Island, South Africa

2.1. Introduction

Biological invaders, especially noxious alien species, are one of the most important threats to biodiversity worldwide (Mack et al. 2000; Winter et al. 2009; Pyšek et al. 2010; Pyšek, Jarošík & Pergl 2011; see also reviews of Mcgeoch et al. 2010 for further references). Invasion success of alien species may be driven by their ability to rapidly adapt to new environments (Pyšek et al. 2011), including those transformed by changing climate (Willis et al. 2008, 2010) or ecosystems artificially altered by humans (Mack et al. 2000; Rice & Emery 2003). The most detrimental ecological impacts of invaders are ecosystem disruption and biodiversity loss, which can lead to global or local extinction (Blackburn et al. 2004; Sax & Gaines 2008; Winter et al. 2009; Davies et al. 2011). As mentioned in chapter one, the control and/or eradication of invasives poses a serious economic burden (U.S. Congress 1993; Versfeld, Le Maitre & Chapman 1998; van Wilgen et al. 2001; Pimentel, Zuniga & Morrison 2005) often ill-afforded in developing countries.

With the current rise in globalisation, and the fast development of transport modes, the introduction of new species to environments is predicted to increase (DAISIE 2009; Hulme 2009; Hulme et al. 2009). This provides a stimulus for the continued investigation of the factors underlying species propensity for successful invasion beyond their natural range (Sagoff 2005).

Such investigations should facilitate the identification of potential invaders (Cadotte, Hamilton & Murray 2009). There is a considerable body of literature focusing on species or habitat traits that predispose introduced species to invasion (Stohlgren et al. 1999; Kolar & Lodge 2002; Booth, Caldwell & Stark 2003; Byers & Noonburg 2003; Levine et al. 2003; van Ruijven, De Deyn & Berendse 2003; Schaefer et al. 2011), although it remains challenging to identify such key traits (Levine et al. 2003). This problem is compounded because invasion success is not determined solely by the traits of the potential invading species, but also by those of the native community being invaded (Darwin 1859; Strauss, Webb & Salamin 2006; Schaefer et al. 2011).

Darwin's naturalisation hypothesis has progressively received greater attention, in part, due to the increasing availability of DNA sequence data (see reviews in Thuiller et al. 2010; Maitner et al. 2011). In the *Origin of Species* (Darwin 1859), Darwin suggested that introduced species, which are more distantly related to natives, maybe more likely to become invasive. He considered that the different evolutionary histories and niches occupied by distant relatives might reduce competition between exotics and natives – this idea is known as Darwin's *naturalisation hypothesis* (Darwin 1859). Since Darwin's hypothesis (Darwin 1859), evolutionary (phylogenetic) relationships have been used to predict potential invaders in a recipient environment (e.g. Schaefer et al. 2011). To date, results of studies that test this hypothesis are mixed. Some studies found Darwin's theory applicable for invasion management (e.g. Strauss, Webb & Salamin 2006; Jiang, Tan & Pu 2010; Schaefer et al. 2011; Van Wilgen & Richardson 2011), and others have challenged its universality (e.g. Cahill et al. 2008; Diez et al. 2008; Maitner et al. 2011). The opposing view is that exotics that are more closely related to natives may be more likely to establish, due greater competitive ability in similar ecological niches (Duncan & Williams 2002; Webb et al. 2002). In fact, the applicability of Darwin's hypothesis may be scale or context dependent (Maitner et al. 2011). Here, we evaluate these ideas, focusing on the flora of Robben Island in South Africa.

2.2 Study Site:

Robben Island is situated 11 km northwest of Table Bay Harbour and 7.5 km west of Blougbergstrand near Table Bay (Figure 2.1). It is 4 km long and 2 km wide, with a total area of 5.07 km^2 (Underhill, Whittington & Calf 2001).

Figure 2.1. Map indicating the position of Robben Island relative to mainland and West Coast Strandveld vegetation (indicated with white arrow).

The island is an ecologically important site as it contains unique habitats supporting large populations of endangered seabirds, including 12% of the world's African Penguin populations (*Spheniscus demersus* L.) and 4% of the Bank Cormorants (*Phalacrocorax neglectus* Wahlberg.) (Underhill, Whittington & Calf 2001) (Figure 2.2).

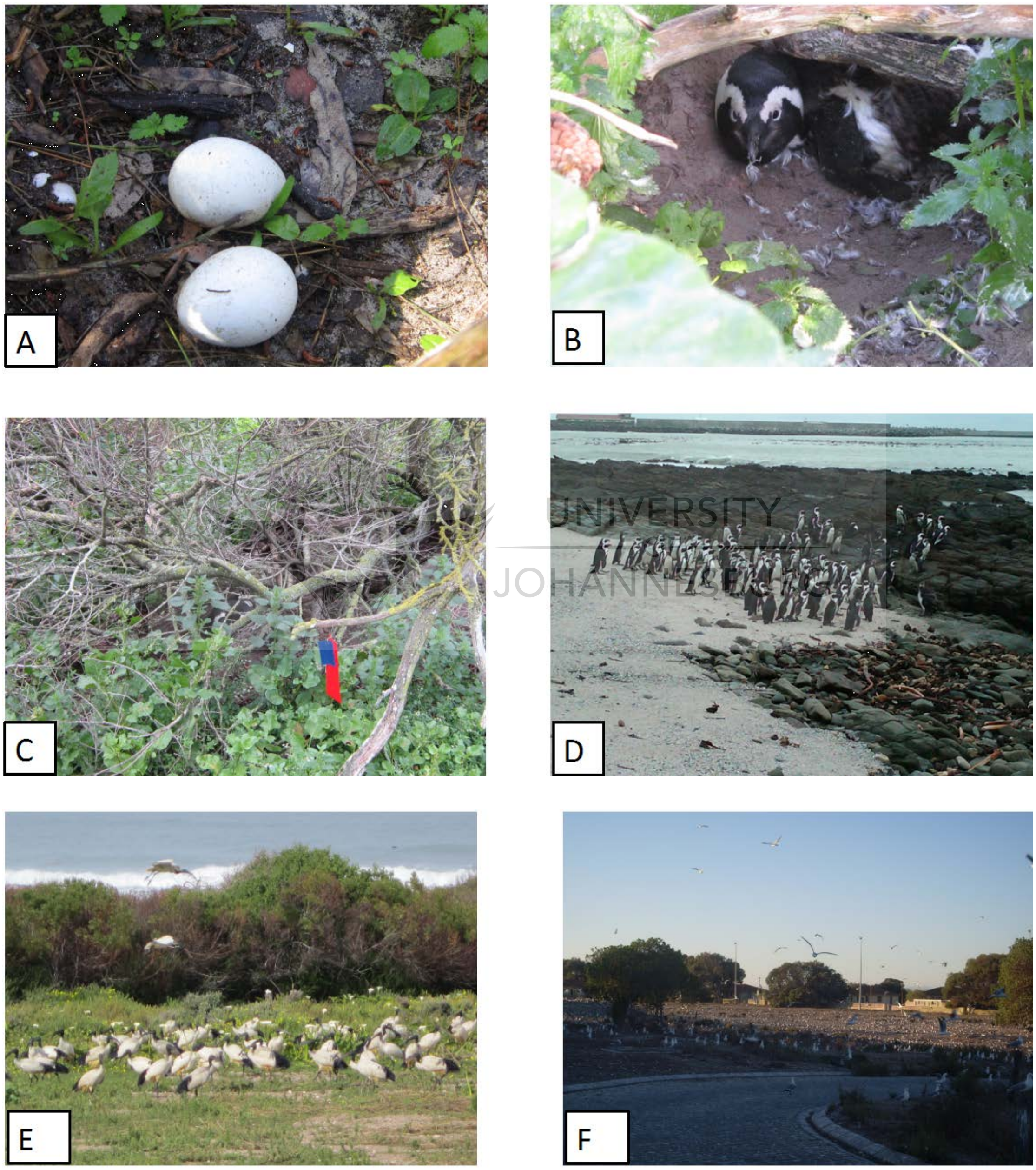


Figure 2.2. Robben Island is an important habitat for avifauna. A & B: Habitat preference and breeding sites of penguins; C: Red and blue tags indicating

sign of penguin breeding colonies; D: A large population of penguins on the island; and E & F showing bird nesting sites.

For over four hundred years, Robben Island has been subject to human activities (infrastructure development, excavations and introduction of alien species for horticultural or agricultural purposes, etc. Figure 2.3). This has severely damaged the natural vegetation (Figures 2.4A & 2.4B).

Figure 2.3. Human induced disturbances to the natural vegetation on the Robben Island. A: Lime quarry; B: Stone quarry; C: Airstrip; and D: Remains of army base.

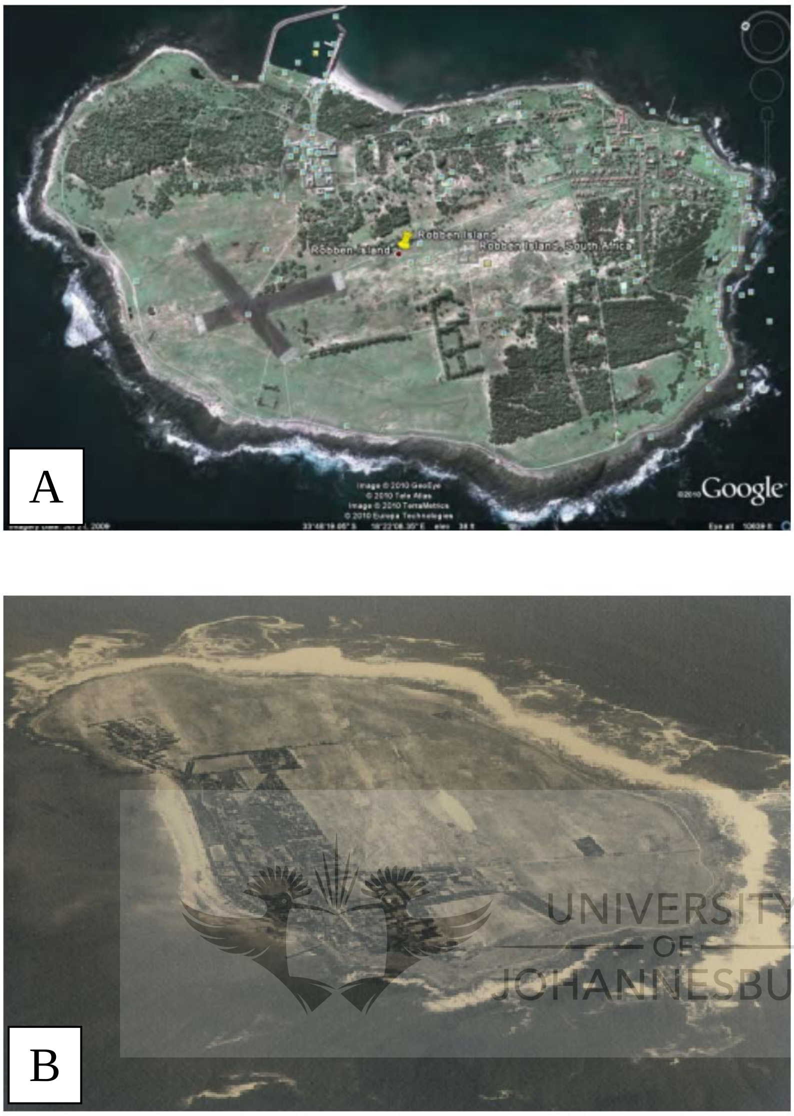


Figure 2.4. Comparison of Robben Island at two different periods. A: Robben Island in its transformed state in 2009; B: 1935, Robben Island in its almost natural state showing little destruction with hardly no trees.

Today, following these human-induced disturbances, at least 42% of the island is occupied by alien vegetation (Chapman, Le Maitre & Holmes 2000)(Figure 2.5).

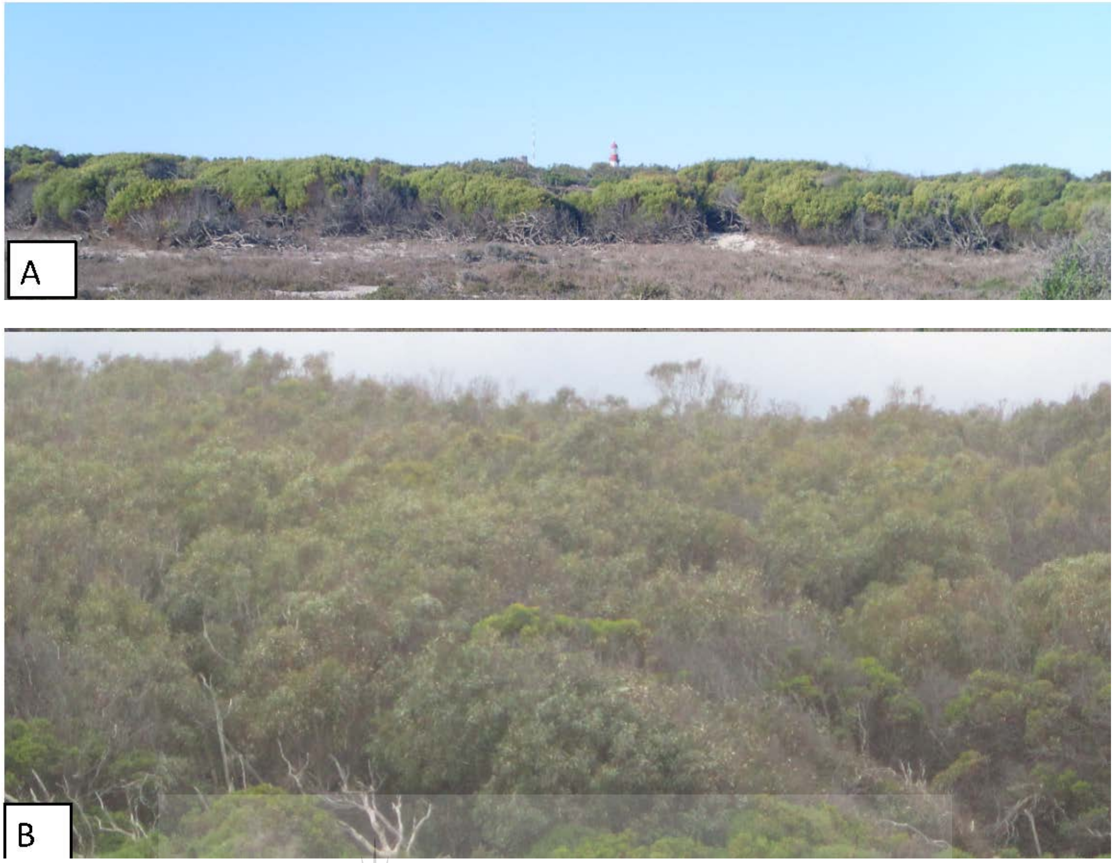


Figure 2.5. Some areas on the island are covered with huge invasions of A: *Acacia cyclops* and B: *Eucalyptus* species.

The concomitant loss of native biodiversity has put at risk the distinctive habitats exploited by endangered birds.

In this study, I carried out a detailed floristic inventory of Robben Island and reconstructed phylogenetic relationships of the native and alien floras based on DNA loci. Combining these data, I examined whether Darwin’s naturalisation hypothesis can be detected in this system.

2.3. Materials and Methods

2.3. 1. Botanical Inventory and Sampling

During December 2010, and April - September 2011, a thorough inventory of the island flora was carried out, recording all native and invasive plant species within a series of study plots described below (Figure 2.6, 2.7).

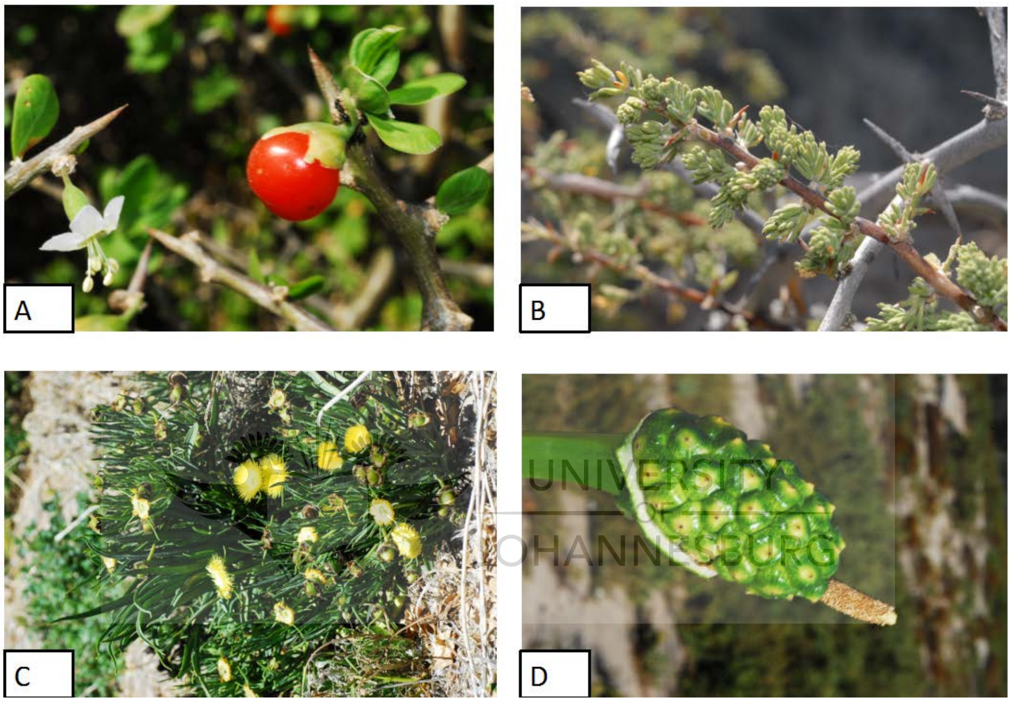
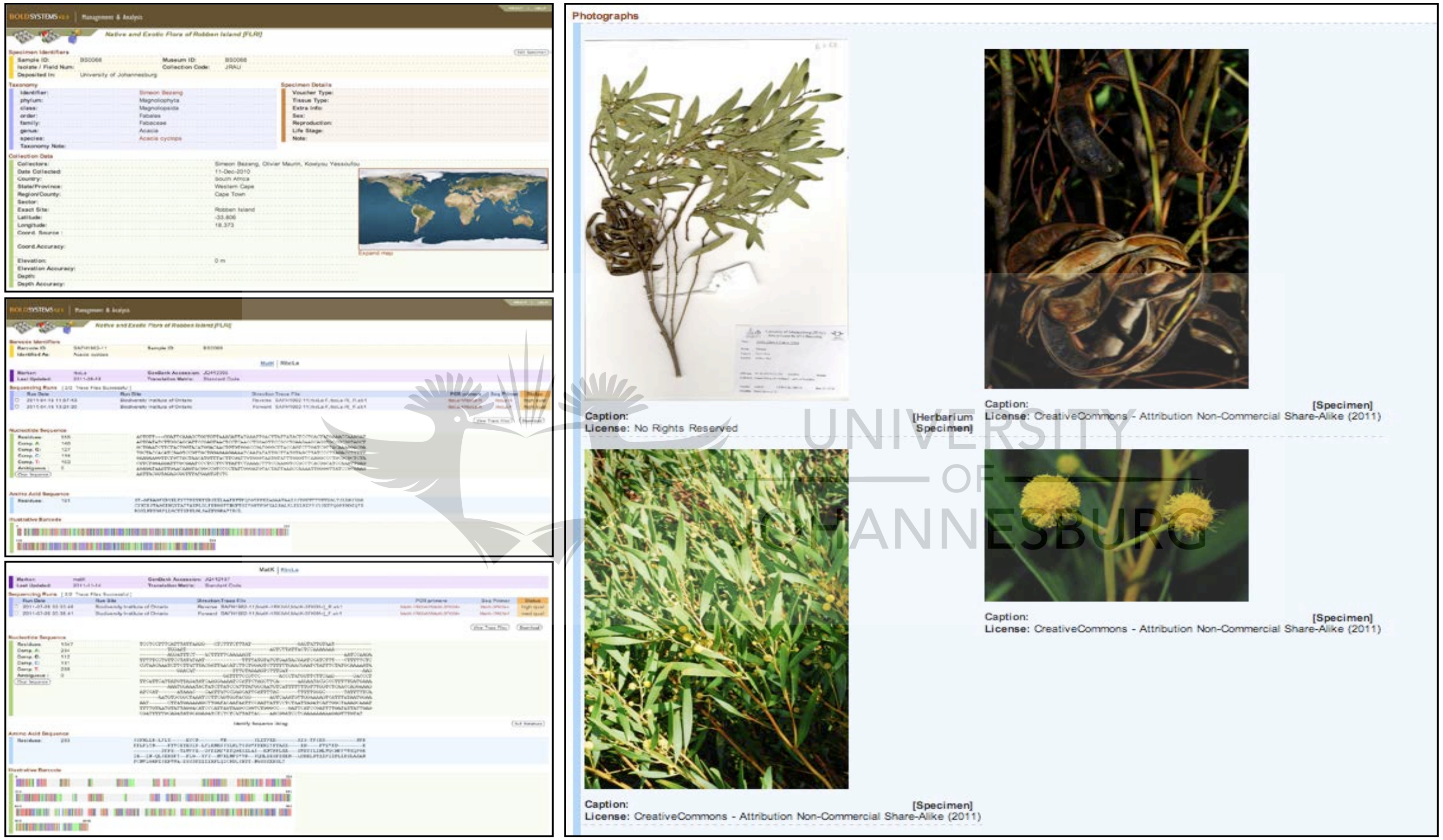


Figure 2.6. Examples of native species found on the island. A: *Lycium ferocissimum*; B: *Asparagus capensis*; C: *Conicosia pugioniformis*; and D: *Zantedeschia aethiopica*. (Photos: O. Maurin).

Figure 2.7. Some invasive species found on the island. A: *Malva parviflora*; B: *Urtica urens*; C: *Nicotiana glauca*; and D: *Mirabilis jalapa*. (Photos: O. Maurin).

Photographs of each species were taken and have been deposited in BOLD (www.boldsystems.org) (Figure 2.8), together with DNA data (see Table 2.1) and geographic coordinates. Voucher specimens of each species have been deposited at the University of Johannesburg Herbarium (JRAU).



Native and Exotic Flora of Robben Island [FLRI]

Specimen Identifiers

Sample ID: BS0068

Museum ID: BS0068

Isolate / Field Num:

Collection Code: JRAU

Deposited In: University of Johannesburg

Taxonomy

Identifier: Simeon Bezeng

phylum: Magnoliophyta

class: Magnoliopsida

order: Fabales

family: Fabaceae

genus: Acacia

species: Acacia cyclops

Taxonomy Note:

Specimen Details

Voucher Type:

Tissue Type:

Extra Info:

Sex:

Reproduction:

Life Stage:

Note:

Collection Data

Collectors: Simeon Bezeng, Olivier Maurin, Kowiyou Yessoufou

Date Collected: 11-Dec-2010

Country: South Africa

State/Province: Western Cape

Region/County: Cape Town

Sector:

Exact Site: Robben Island

Latitude: -33.806

Longitude: 18.373

Coord. Source :

Coord.Accuracy:

Elevation: 0 m

Elevation Accuracy:

Depth:

Depth Accuracy:

Photographs

Caption: [Herbarium Specimen]

License: No Rights Reserved

Caption: [Specimen]

License: CreativeCommons - Attribution Non-Commercial Share-Alike (2011)

Caption: [Specimen]

License: CreativeCommons - Attribution Non-Commercial Share-Alike (2011)

Caption: [Specimen]

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Figure 2.8. DNA sequences, collection data and pictures available on BOLD for the invasive species, (here *Acacia cyclops* is showed).

In the inventory, I recorded 170 species, of which 83 were classified as invasive and six were unidentified (Table 2.1). Classification of invasive species followed Henderson (2007) and observations from local conservation authorities.

Table 2.1. List of taxa with voucher information and GenBank accession numbers for each DNA region. Categories: ‘I’=invasive plants, ‘N’=native, ‘G’=garden plants, ‘O’=unknown, and ‘N/A’=not applicable. Sequences downloaded from GenBank: [1]unpublished data; [2]Lledo & Davis 2004; [3]Hilu et al. 2003; [4]Treutlein et al. 2003; [5]Schaefer et al. 2011; [6]Cohen & Davis 2009.

Family	**Taxa**	**Category**	**Voucher, Herbarium Acronym**	**BOLD Accession Number**	**GenBank Accession Number**	
					rbcLa	***matK***
Asparagaceae	*Agave americana* L.	I	*BS0127*, JRAU	SAFH2525-11	JQ412308	JQ412190
Asparagaceae	*Agave sp*	I	*BS0064*, JRAU	SAFH2516-11	JQ412307	JQ412189
Asparagaceae	*Yucca gloriosa* L.	I	*BS0075*, JRAU	SAFH2518-11	JQ412437	JQ412303
Asparagaceae	*Yucca filamentosa* L.	I	*BS0126*, JRAU	SAFH2524-11	JQ412436	JQ412302
Aizoaceae	*Conicosia pugioniformis* (L.) N.E.Br.	N	*BS0093*, JRAU	SAFH1980-11	JQ412345	JQ412226
Aizoaceae	*Delosperma* sp.	O	*BS0116*, JRAU	SAFH2000-11	JQ412351	JQ412231
Aizoaceae	*Disphyma crassifolium* (L.) L. Bolus	O	*BS0138*, JRAU	SAFH2015-11	JQ412353	JQ412233
Aizoaceae	*Mesembryanthemum crystallinum* L.	N	*BS0113*, JRAU	SAFH1999-11	JQ412389	JQ412264
Aizoaceae	*Tetragonia decumbens* Mill.	N	*BS0154*, JRAU	SAFH2027-11	JQ412427	JQ412294
Aizoaceae	*Tetragonia fruticosa* L.	N	*BS0071*, JRAU	SAFH1964-11	JQ412428	JQ412295
Amaranthaceae	*Amaranthus deflexus* L.	O	*BS0148*, JRAU	SAFH2022-11	JQ412313	JQ412195
Amaranthaceae	*Sarcocornia perennis* (Mill.) A.J.Scott	N	*BS0135*, JRAU	—	DQ468646.1[1]	DQ468646.1[1]
Amaryllidaceae	*Allium oleraceus* L.	O	*BS0272*, JRAU	—	AY101314.1[2]	AY101314.1[2]
Amaryllidaceae	*Haemanthus coccineus* L.	N	*BS0252*, JRAU	SAFH2890-11	JQ412314	JQ412196
Amaryllidaceae	*Narcissus elegans* (Haw.)	I	*BS0246*, JRAU	SAFH2884-11	AJ581389[3]	AJ581389[3]

Family	Taxa	Category	Voucher, Herbarium Acronym	BOLD Accession Number	GenBank Number	Accession
					rbcLa	*matK*
	Spach					
Amborellaceae	*Amborella trichopoda* Baill	N/A	—	—	AF543721[1]	AF543721[1]
Anacardiaceae	*Harpephyllum caffrum* Bernh. ex Krauss	O	*BS0058*, JRAU	SAFH1954-11	JQ412371	JQ412249
Anacardiaceae	*Schinus terebinthifolia* Raddi	I	*BS0098*, JRAU	SAFH1984-11	JQ412419	JQ412287
Apiaceae	*Foeniculum vulgare* Mill.	O	*BS0076*, JRAU	SAFH1967-11	JQ412367	JQ412247
Apocynaceae	*Acokanthera oppositifolia* (Lam.) Codd	N	*BS0162*, JRAU	SAFH2035-11	JQ412306	JQ412188
Apocynaceae	*Carissa macrocarpa* (Eckl.) A.DC.	N	*BS0059*, JRAU	SAFH1955-11	JQ412334	JQ412217
Apocynaceae	*Catharanthus roseus* (L.) G.Don	I	*BS0161*, JRAU	SAFH2034-11	JQ412337	JQ412220
Apocynaceae	*Nerium oleander* L.	I	*BS0125*, JRAU	SAFH2007-11	JQ412398	JQ412271
Araceae	*Zantedeschia aethiopica* (L.) Spreng.	N	*BS0072*, JRAU	SAFH2517-11	JQ412438	JQ412304
Araliaceae	*Hedera helix* L.	I	*BS0160*, JRAU	SAFH2033-11	JQ412372	JQ412250
Araucariaceae	*Araucaria heterophylla* (Salisb.) Franco	I	*BS0114*, JRAU	—	—	—
Arecaceae	*Phoenix canariensis* Chabaud	I	*BS0121*, JRAU	SAFH2523-11	JQ412407	JQ412277
Arecaceae	*Washingtonia robusta* H.Wendl.	I	*BS0120*, JRAU	SAFH2522-11	JQ412435	JQ412301
Asparagaceae	*Asparagus capensis* L.	N	*BS0131*, JRAU	SAFH2526-11	JQ412322	JQ412204
Asteraceae	*Arctotheca calendula* (L.)	N	*BS0137*, JRAU	SAFH2014-11	JQ412316	JQ412198

Family	Taxa	Category	Voucher, Herbarium Acronym	BOLD Accession Number	GenBank Number	Accession
					rbcLa	*matK*
	Levyns					
Asteraceae	*Arctotheca papulifolia* (Berg) T Norl	N	*BS0099*, JRAU	SAFH2881-11	JQ412381	—
Asteraceae	*Arctotheca* sp.	N	*BS0090*, JRAU	SAFH1978-11	JQ412327	JQ412211
Asteraceae	*Artemisia afra* Jacq. ex Willd.	I	*BS0167*, JRAU	SAFH2532-11	JQ412318	JQ412200
Asteraceae	*Brachylaena discolor* DC.	O	*BS0103*, JRAU	SAFH1989-11	JQ412332	JQ412216
Asteraceae	*Chrysanthemoides monilifera* (L.) Norl.	O	*BS0112*, JRAU	SAFH1998-11	—	JQ412207
Asteraceae	*Cotula coronopifolia* L.	N	*BS0276*, JRAU	SAFH2884-11	JQ412382	JQ412258
Asteraceae	*Dittrichia graveolens* (L.) Greuter	O	*BS0144*, JRAU	SAFH2019-11	—	JQ412209
Asteraceae	*Hypochoeris glabra* L.	N	*BS0250*, JRAU	SAFH2888-11	JQ412374	JQ412252
Asteraceae	*Metalasia densa* (Lam.) P.O.Karis	N	*BS0166*, JRAU	SAFH2039-11	JQ412390	JQ412265
Asteraceae	*Metalasia* sp.	N	*BS0170*, JRAU	SAFH2042-11	JQ412323	—
Asteraceae	*Oncosiphon grandiflorum* (Thunb.) Källersjö	N	*BS0248*, JRAU	SAFH2886-11	JQ412325	JQ412206
Asteraceae	*Oncosiphon suffruticosum* (L.) Källersjö	N	*BS0054*, JRAU	SAFH1951-11	JQ412401	JQ412274
Asteraceae	*Pseudognaphalium luteoalbum* (L.) Hilliard & B.L.Burtt	N	*BS0262*, JRAU	—	HM850635.1[5]	—
Asteraceae	*Senecio maritimus* L.f.	N	*BS0078*, JRAU	SAFH1969-11	JQ412424	JQ412291
Asteraceae	*Sonchus oleraceus* (L.) L.	N	*BS0257*, JRAU	SAFH2895-11	—	JQ412208

Family	**Taxa**	**Category**	**Voucher, Herbarium Acronym**	**BOLD Accession Number**	**GenBank Accession Number**	
					rbcLa	***matK***
Asteraceae	*Sonchus* sp.	N	*BS0086*, JRAU	SAFH1974-11	JQ412326	JQ412210
Boraginaceae	*Echium vulgare* L.	I	*BS0289*, JRAU	—	FJ827257[6]	FJ827257[6]
Brassicaceae	*Aurinia saxatilis* (L.) Desv.	I	*BS0065*, JRAU	SAFH1959-11	JQ412329	JQ412213
Brassicaceae	Indet.	I	*BS0244*, JRAU	SAFH2882-11	JQ412413	JQ412282
Brassicaceae	*Rapistrum rugosum* (L.) All.	I	*BS0263*, JRAU	—	HM850756.1[5]	HM850756.1[5]
Cactaceae	*Opuntia stricta* (Haw.) Haw.	I	*BS0106*, JRAU	SAFH1992-11	JQ412402	JQ412275
Caryophyllaceae	*Dianthus caryophyllus* L.	I	*BS0152*, JRAU	SAFH2025-11	JQ412352	JQ412232
Caryophyllaceae	*Polycarpon tetraphyllum* (L.) L.	N	*BS0134*, JRAU	SAFH2011-11	JQ412335	JQ412218
Celastraceae	*Catha edulis* (Vahl) Endl.	I	*BS0153*, JRAU	SAFH2026-11	JQ412336	JQ412219
Amaranthaceae	*Bassia diffusa* (Thunb.) Kuntze	I	*BS0136*, JRAU	SAFH2013-11	JQ412312	JQ412194
Amaranthaceae	*Chenopodium album* L.	I	*BS0082*, JRAU	SAFH1971-11	JQ412341	JQ412222
Amaranthaceae	*Chenopodium murale* L.	I	*BS0067*, JRAU	SAFH1961-11	JQ412342	JQ412223
Amaranthaceae	*Atriplex rosea* L.	I	*BS0087*, JRAU	SAFH1975-11	JQ412340	JQ412221
Amaranthaceae	*Exomis microphylla* (Thunb.) Aellen	O	*BS0128*, JRAU	SAFH2008-11	JQ412363	JQ412243
Amaranthaceae	*Salsola kali* L.	I	*BS0066*, JRAU	SAFH1960-11	JQ412416	—
Colchicaceae	*Indet.*	N	*BS0243*, JRAU	SAFH2881-11	JQ412381	—
Combretaceae	*Combretum kraussii* Hochst.	G	*BS0095*, JRAU	SAFH1982-11	JQ412344	JQ412225
Crassulaceae	*Cotyledon orbiculata* L.	N	*BS0129*, JRAU	SAFH2009-11	JQ412346	JQ412227
Crassulaceae	Indet.	O	*BS0083*, JRAU	SAFH1972-11	JQ412347	—

Family	**Taxa**	**Category**	**Voucher, Herbarium Acronym**	**BOLD Accession Number**	**GenBank Accession Number**	
					rbcLa	***matK***
Crassulaceae	*Kalanchoe beharensis* Drake	G	*BS0119*, JRAU	SAFH2003-11	JQ412375	—
Cucurbitaceae	*Cucumis anguria* L.	O	*BS0150*, JRAU	SAFH2024-11	JQ412348	JQ412228
Ebanaceae	*Euclea racemosa* L.	N	*BS0073*, JRAU	SAFH1965-11	JQ412361	JQ412241
Euphorbiaceae	*Euphorbia drummondii* Boiss.	O	*BS0157*, JRAU	SAFH2030-11	JQ412338	—
Euphorbiaceae	*Euphorbia peplus* L.	I	*BS0149*, JRAU	SAFH2023-11	JQ412362	JQ412242
Fabaceae	*Acacia cyclops* G.Don	I	*BS0068*, JRAU	SAFH1962-11	JQ412305	JQ412187
Fabaceae	*Erythrina caffra* Thunb.	N	*BS0057*, JRAU	SAFH1953-11	JQ412356	JQ412236
Geraniaceae	*Erodium moschatum* (L.) L'Hér.	I	*BS0245*, JRAU	—	HM850905.1[5]	HM850905.1[5]
Geraniaceae	*Geranium incanum* Burm.f.	O	*BS0109*, JRAU	SAFH1995-11	JQ412369	—
Geraniaceae	*Geranium molle* L.	I	*BS0147*, JRAU	SAFH2021-11	JQ412370	JQ412248
Geraniaceae	*Pelargonium capitatum* (L.) L'Hér.	N	*JWB507*, JRAU	SAFH2048-11	JQ412405	HM850906[5]
Geraniaceae	*Pelargonium cucullatum* subsp. *tabulare* Volschenk	N	*BS0111*, JRAU	SAFH1997-11	JQ412406	—
Geraniaceae	Indet.	I	*BS0168*, JRAU	SAFH2040-11	JQ412368	—
Hemerocallidaceae	*Phormium tenax* J.R.Forst. & G.Forst.	I	*BS0141*, JRAU	SAFH2528-11	JQ412408	JQ412278
Iridaceae	*Ferraria crispa* Burm.	N	*BS0255*, JRAU	SAFH2893-11	JQ412339	—
Iridaceae	*Romulea rosea* (L.) Eckl.	N	*BS0249*, JRAU	SAFH2887-11	JQ412414	JQ412283
Lamiaceae	*Leonotis leonurus* (L.) R.Br.	N	*BS0055*, JRAU	SAFH1952-11	JQ412377	JQ412254
Lamiaceae	*Salvia lanceolata* Lam.	N	*BS0110*, JRAU	—	—	—
Lilliaceae	Indet.	N	*BSO242,* JRAU	SAFH2896-11	JQ412409	JQ412279

Family	**Taxa**	**Category**	**Voucher, Herbarium Acronym**	**BOLD Accession Number**	**GenBank Number**	**Accession**
					rbcLa	***matK***
Malvaceae	*Hibiscus rosa-sinensis* L.	I	*BS0104*, JRAU	SAFH1990-11	JQ412373	JQ412251
Malvaceae	*Lagunaria patersonia* (Andrews) G.Don	I	*BS0107*, JRAU	SAFH1993-11	JQ412376	JQ412253
Malvaceae	*Malva parviflora* L.	I	*BS0092*, JRAU	SAFH1979-11	JQ412388	JQ412263
Malvaceae	*Malva neglecta* Wallr.	I	*BS0155*, JRAU	SAFH2028-11	JQ412387	JQ412262
Moraceae	*Ficus carica* L.	I	*BS0084*, JRAU	SAFH1973-11	JQ412365	JQ412245
Moraceae	*Ficus microcarpa* L.f.	I	*BS0077*, JRAU	SAFH1968-11	JQ412366	JQ412246
Moraceae	*Morus alba* L.	I	*BS0124*, JRAU	SAFH2006-11	JQ412393	JQ412268
Myrtaceae	*Callistemon viminalis* (Sol. ex Gaertn.) G.Don ex Loudon	I	*BS0118*, JRAU	SAFH2002-11	JQ412333	JQ412237
Myrtaceae	*Eucalyptus spBS1.*	I	*BS0063*, JRAU	SAFH1958-11	JQ412357	JQ412237
Myrtaceae	*Eucalyptus sp2.*	I	*BS0079*, JRAU	SAFH1970-11	JQ412359	JQ412239
Myrtaceae	*Eucalyptus sp3.*	I	*BS0130*, JRAU	SAFH2010-11	JQ412360	JQ412240
Myrtaceae	*Eucalyptus sp4.*	I	*BS0159*, JRAU	SAFH2032-11	JQ412358	JQ412238
Myrtaceae	*Leptospermum laevigatum* (Gaertn.) F.Muell.	I	*BS0158*, JRAU	SAFH2031-11	JQ412378	JQ412255
Myrtaceae	*Metrosideros excelsa* Sol. ex Gaertn.	I	*BS0097*, JRAU	SAFH1983-11	JQ412391	JQ412266
Nyctaginaceae	*Bougainvillea glabra* Choisy	I	*BS0108*, JRAU	SAFH1994-11	JQ412331	JQ412215
Nyctaginaceae	*Mirabilis jalapa* L.	I	*BS0088*, JRAU	SAFH1976-11	JQ412392	JQ412267
Oleaceae	*Ligustrum lucidum* W.T.Aiton	I	*BS0102*, JRAU	SAFH1988-11	JQ412380	JQ412257
Oleaceae	Indet.	I	*BS0146*, JRAU	SAFH2020-11	JQ412417	JQ412285
Oleaceae	*Olea europaea* subsp. *cuspidata* (Wall. & G.Don)	N	*BS0123*, JRAU	SAFH2005-11	JQ412400	JQ412273

Family	Taxa	Category	Voucher, Herbarium Acronym	BOLD Accession Number	GenBank Accession Number	
					rbcLa	***matK***
	Cif.					
Oxalidaceae	*Oxalis pes-caprae* L.	I	*BS0251*, JRAU	—	HM851020.1[5]	HM851020.1[5]
Poaceae	*Arundo donax* L.	I	*BS0142*, JRAU	SAFH2529-11	JQ412319	JQ412201
Poaceae	*Avena sativa* L.	I	*BS0080*, JRAU	SAFH2519-11	JQ412330	JQ412214
Poaceae	*Bromus diandrus* Roth	I	*BS0273*, JRAU	—	HM849828[5]	HM850584[5]
Poaceae	*Cynodon dactylon* (L.) Pers.	N	*BS0132*, JRAU	SAFH2527-11	JQ412349	JQ412229
Polygalaceae	*Polygala myrtifolia* L.	G	*BS0165*, JRAU	SAFH2038-11	JQ412410	—
Polygalaceae	*Muraltia satureioides* Burch. ex DC.	I	*BS0163*, JRAU	SAFH2036-11	JQ412394	—
Polygalaceae	*Muraltia spinosa* (L.) F.Forest & J.C.Manning	I	*BS0164*, JRAU	SAFH2037-11	JQ412395	—
Portulacaceae	*Portulacaria afra* Jacq.	N	*BS0169*, JRAU	SAFH2041-11	JQ412411	JQ412280
Restionaceae	*Chondropetalum tectorum* (L.f.) Raf	O	*BS0151*, JRAU	SAFH2531-11	JQ412343	JQ412224
Restionaceae	*Thamnochortus spicigerus* (Thunb.) Spreng.	I	*BS0171*, JRAU	SAFH2533-11	JQ412429	JQ412296
Salicaceae	*Dovyalis caffra* (Hook. f. & Harv.) Warb.	N	*BS0094*, JRAU	SAFH1981-11	JQ412354	JQ412234
Sapotaceae	*Sideroxylon inerme* L.	N	*BS0117*, JRAU	SAFH2001-11	JQ412421	JQ412288
Scrophulariaceae	*Myoporum laetum* G.Forst.	I	*BS0060*, JRAU	SAFH1956-11	JQ412397	JQ412270
Scrophulariaceae	*Myoporum* cf. *laetum* G.Forst.	I	*BS0122*, JRAU	SAFH2004-11	JQ412396	JQ412269
Scrophulariaceae	*Zalusianskya villosa* F.W. Schmidt	N	*BS0247*, JRAU	SAFH2885-11	JQ412324	JQ412205

Family	Taxa	Category	Voucher, Herbarium Acronym	BOLD Accession Number	GenBank Accession Number	
					rbcLa	*matK*
Solanaceae	*Datura stramonium* L.	I	*BS0089*, JRAU	SAFH1977-11	JQ412350	JQ412230
Solanaceae	*Lycium afrum* L.	N	*BS0140*, JRAU	SAFH2017-11	JQ412384	JQ412259
Solanaceae	*Lycium ferocissimum* Miers	N	*BS0069*, JRAU	SAFH1963-11	JQ412385	JQ412260
Solanaceae	*Lycopersicon esculentum* Mill.	I	*BS0156*, JRAU	SAFH2029-11	JQ412386	JQ412261
Solanaceae	*Nicotiana glauca* Graham	I	*BS0101*, JRAU	SAFH1987-11	JQ412399	JQ412272
Solanaceae	*Solanum linnaeanum* Hepper & P.-M.L.Jaeger	N	*BS0143*, JRAU	SAFH2018-11	JQ412422	JQ412289
Solanaceae	*Solanum nigrum* L.	I	*BS0100*, JRAU	SAFH1986-11	JQ412423	JQ412290
Strelitziaceae	*Strelitzia reginae* Banks ex Aiton	G	*BS0271*, JRAU	SAFH2898-11	JQ412425	JQ412292
Tamaricaceae	*Tamarix chinensis* Lour.	I	*BS0105*, JRAU	SAFH1991-11	JQ412426	JQ412293
Tecophilaeaceae	*Cyanella orchidiformis* Jacq.	N	*BS0261*, JRAU	SAFH2896-11	JQ412409	JQ412279
Tropaeolaceae	*Tropaeolum majus* L.	I	*BS0282*, JRAU	—	HM850758.1^{5}	HM850758.1^{5}
Urticaceae	*Urtica urens* L.	I	*BS0062*, JRAU	SAFH1957-11	JQ412434	HM851111.1^{5}
Xanthorrheaceae	*Aloe arborescens* Mill.	N	*BS0270*, JRAU	SAFH2897-11	—	AY323722^{4}
Xanthorrheaceae	*Aloe maculata* All.	N	*BS0145*, JRAU	SAFH2530-11	JQ412311	JQ412193
Xanthorrheaceae	*Trachyandra ciliata* (L.f.) Kunth	N	*BS0256*, JRAU	SAFH2894-11	JQ412431	JQ412298
Xanthorrheaceae	*Trachyandra divaricata* (Jacq.) Kunth	N	*BS0091*, JRAU	SAFH2520-11	JQ412432	JQ412299

This floristic survey differs from the previous one by the Council for Scientific and Industrial Research (CSIR) in 2010: I did not find 79 species from the CSIR inventory (44 natives, 25 invasive and 10 garden plants). The mismatch between the inventories is likely to be due to differences in the period of survey; we did not collect during spring (October-November), and therefore some annual species were not recorded (Table 2.2). The island is currently experiencing extensive vegetation regeneration and some aliens have been cleared. However, we found 38 extra taxa, i.e. those missing in the CSIR inventory.

Table 2.2. Inventory of all plants recorded on Robben Island (2010 & 2011). R = Recorded, N/R = Not Recorded, I = Invasive, N = Native, O = Other, G = Garden.

APG III Family	**All plants recorded on Island (2010 & 2011)**	**2010 CSIR Inventory**	**2010- 2011 BS Inventory**	**I/N/G/O**	**Voucher**
Aizoaceae	*Aizoon canariense* L.	R	N/R	I	—
Aizoaceae	*Carpobrotus acinaciformis* (L.) L.Bolus	R	N/R	N	—
Aizoaceae	*Conicosia pugioniformis* (L.) N.E.Br.	N/R	R	N	*BS0093*, JRAU
Aizoaceae	*Delosperma* N.E.Br. sp.1	N/R	R	O	*BS0116*, JRAU
Aizoaceae	*Disphyma crassifolium* (L.) L.Bolus	N/R	R	O	*BS0138*, JRAU
Aizoaceae	*Dorotheanthus apetalus* (L.f.) N.E.Br.	R	N/R	N	—
Aizoaceae	*Drosanthemum floribundum* (Haw.) Schwantes	R	N/R	N	—
Aizoaceae	*Erepsia dunensis* (Sond.) Klak	R	N/R	N	—
Aizoaceae	*Galenia secunda* (L.) Sond.	R	N/R	N	—
Aizoaceae	*Malephora purpureocrocea* Schwantes	N/R	R	O	*BS0239*, JRAU
Aizoaceae	*Mesembryanthemum crystallinum* L.	N/R	R	N	*BS0113*, JRAU
Aizoaceae	*Mesembryanthemum nodiflorum* L.	N/R	R	N	*BS0233*, JRAU
Aizoaceae	*Mesembryanthemum* sp.1	R	N/R	N	—
Aizoaceae	*Mesembryanthemum* sp.2	R	N/R	N	—

APG III Family	**All plants recorded on Island (2010 & 2011)**	**2010 CSIR Inventory**	**2010- 2011 BS Inventory**	**I/N/G/O**	**Voucher**
Aizoaceae	*Phyllobolus canaliculatus* (Haw.) Bittrich	R	N/R	N	—
Aizoaceae	*Tetragonia decumbens* Mill.	N/R	R	N	*BS0154*, JRAU
Aizoaceae	*Tetragonia fruticosa* L.	N/R	R	N	*BS0071*, JRAU
Amaranthaceae	*Amaranthus deflexus* L.	R	R	O	*BS0148*, JRAU
Amaranthaceae	*Guilleminea densa* (Willd. ex Schult.) Moq.	R	R	I	*BS0115*, JRAU
Amaranthaceae	*Sarcocornia* sp.1	N/R	R	N	*BS0241*, JRAU
Amaranthaceae	*Sarcocornia perennis* (Mill.) A.J.Scott	N/R	R	N	*BS0135*, JRAU
Amaranthaceae	*Atriplex canescens* (Pursh) Nutt.	N/R	R	I	*BS0240*, JRAU
Amaranthaceae	*Atriplex prostrata* Boucher ex DC.	N/R	R	I	*BS0234*, JRAU
Amaranthaceae	*Atriplex rosea* L.	N/R	R	I	*BS0087*, JRAU
Amaranthaceae	*Bassia diffusa* (Thunb.) Kuntze	N/R	R	I	*BS0136*, JRAU
Amaranthaceae	*Chenopodium album* L.	N/R	R	I	*BS0082*, JRAU
Amaranthaceae	*Chenopodium murale* L.	N/R	R	I	*BS0067*, JRAU
Amaranthaceae	*Dysphania botrys* (L.) Mosyakin & Clemants	N/R	R	I	*BS0230*,

APG III Family	**All plants recorded on Island (2010 & 2011)**	**2010 CSIR Inventory**	**2010- 2011 BS Inventory**	**I/N/G/O**	**Voucher**
					JRAU
Amaranthaceae	*Exomis microphylla* (Thunb.) Aellen	N/R	R	O	*BS0128*, JRAU
Amaranthaceae	*Salicornia meyeriana* Moss	R	N/R	N	—
Amaranthaceae	*Salsola kali* L.	N/R	R	I	*BS0066*, JRAU
Amaryllidaceae	*Allium oleraceum* L.	R	N/R	I	—
Amaryllidaceae	*Allium* sp.1	R	N/R	I	—
Amaryllidaceae	*Amaryllis belladonna* L.	R	N/R	N	—
Amaryllidaceae	*Brunsvigia orientalis* (L.) Aiton ex Eckl.	R	N/R	N	—
Amaryllidaceae	*Haemanthus coccineus* L.	N/R	R	N	*BS0252*, JRAU
Amaryllidaceae	*Leucojum aestivum* L.	N/R	R	O	*BS0272*, JRAU
Amaryllidaceae	*Narcissus elegans* (Haw.) Spach	N/R	R	I	*BS0246*, JRAU
Anacardiaceae	*Harpephyllum caffrum* Bernh. ex C.Krauss	N/R	R	O	*BS0058*, JRAU
Anacardiaceae	*Schinus molle* L.	R	N/R	I	—
Anacardiaceae	*Schinus terebinthifolia* Raddi	N/R	R	I	*BS0098*, JRAU
Apiaceae	*Capnophyllum africanum* (L.) Gaertn.	R	N/R	N	—
Apiaceae	*Foeniculum vulgare* Mill.	N/R	R	I	*BS0076*, JRAU
Apiaceae	*Torilis arvensis* (Huds.) Link	N/R	R	N	*BS0279*, JRAU

APG III Family	All plants recorded on Island (2010 & 2011)	2010 CSIR Inventory	2010- 2011 BS Inventory	I/N/G/O	Voucher
Apocynaceae	*Acokanthera oppositifolia* (Lam.) Codd	N/R	R	N	*BS0162*, JRAU
Apocynaceae	*Asclepia* sp.1	R	N/R	N	—
Apocynaceae	*Carissa macrocarpa* (Eckl.) A.DC.	N/R	R	N	*BS0059*, JRAU
Apocynaceae	*Catharanthus roseus* (L.) G.Don	N/R	R	I	*BS0161*, JRAU
Apocynaceae	*Cynanchum zeyheri* Schltr.	R	N/R	N	—
Apocynaceae	*Gomphocarpus fruticosus* (L.) W.T.Aiton	R	N/R	N	—
Apocynaceae	*Nerium oleander* L.	N/R	R	I	*BS0125*, JRAU
Apocynaceae	*Orbea variegata* (L.) Haw.	R	N/R	N	—
Araceae	*Lemna gibba* L.	R	N/R	N	—
Araceae	*Zantedeschia aethiopica* (L.) Spreng.	N/R	R	N	*BS0072*, JRAU
Araliaceae	*Hedera helix* L.	N/R	R	I	*BS0160*, JRAU
Araucariaceae	*Araucaria heterophylla* (Salisb.) Franco	N/R	R	I	*BS0114*, JRAU
Arecaceae	*Phoenix canariensis* Chabaud	N/R	R	I	*BS0121*, JRAU
Arecaceae	*Phoenix reclinata* Jacq.	R	N/R	I	—
Arecaceae	*Washingtonia robusta* H.Wendl.	N/R	R	I	*BS0120*, JRAU
Asparagaceae	*Agave americana* L.	N/R	R	I	*BS0127*, JRAU

APG III Family	All plants recorded on Island (2010 & 2011)	2010 CSIR Inventory	2010- 2011 BS Inventory	I/N/G/O	Voucher
Asparagaceae	*Agave sp*	N/R	R	I	*BS0064*, JRAU
Asparagaceae	*Yucca filamentosa* L.	N/R	R	I	*BS0126*, JRAU
Asparagaceae	*Yucca gloriosa* L.	N/R	R	I	*BS0075*, JRAU
Asparagaceae	*Asparagus asparagoides* (L) Willd	R	N/R	N	—
Asparagaceae	*Asparagus capensis* L.	N/R	R	N	*BS0131*, JRAU
Asparagaceae	*Asparagus* sp.1	R	N/R	N	—
Asteraceae	*Arctotheca calendula* (L.) Levyns	N/R	R	N	*BS0137*, JRAU
Asteraceae	*Arctotheca* sp.1	N/R	R	N	*BS0090*, JRAU
Asteraceae	*Arctotis hirsuta* (Harv.) Beauverd	R	N/R	N	—
Asteraceae	*Artemisia afra Jacq. ex Willd.*	N/R	R	I	*BS0167*, JRAU
Asteraceae	Asteraceae Indet.1	N/R	R	O	*BS0253*, JRAU
Asteraceae	Asteraceae Indet.2	N/R	R	O	*BS0254*, JRAU
Asteraceae	Asteraceae Indet.3	N/R	R	O	*BS0275*, JRAU
Asteraceae	Asteraceae Indet.4	N/R	R	O	*BS0269*, JRAU
Asteraceae	Asteraceae Indet.5	N/R	R	O	*BS0293*,

APG III Family	All plants recorded on Island (2010 & 2011)	2010 CSIR Inventory	2010- 2011 BS Inventory	I/N/G/O	Voucher
					JRAU
Asteraceae	*Berkheya rigida* (Thunb.) "Bolus & Wolley-Dod ex Ewart, Jean White & B.Rees"	R	N/R	N	—
Asteraceae	*Brachylaena discolor* DC.	N/R	R	O	*BS0103*, JRAU
Asteraceae	*Chrysanthemoides monilifera* (L.) Norl.	N/R	R	O	*BS0112*, JRAU
Asteraceae	*Chrysanthemum frutescens* L.	R	N/R	I	—
Asteraceae	*Conyza bonariensis* (L.) Cronquist	N/R	R	I	*BS0259*, JRAU
Asteraceae	*Cotula coronopifolia* L.	N/R	R	N	*BS0276*, JRAU
Asteraceae	*Cotula filifolia* Thunb.	R	N/R	N	—
Asteraceae	*Dimorphotheca pluvialis* (L.) Moench	N/R	R	N	*BS0250*, JRAU
Asteraceae	*Dittrichia graveolens (L.) Greuter*	N/R	R	O	*BS0144*, JRAU
Asteraceae	*Gazania hybrid cultivars*	R	N/R	N	—
Asteraceae	*Helichrysum patulum* (L.) D.Don	R	N/R	N	—
Asteraceae	*Matricaria* sp.1	R	N/R	I	—
Asteraceae	*Metalasia densa* (Lam.) P.O.Karis	N/R	R	N	*BS0166*, JRAU
Asteraceae	*Metalasia* sp.1	N/R	R	N	*BS0170*, JRAU
Asteraceae	*Oncosiphon grandiflorum* (Thunb.) Källersjö	N/R	R	N	*BS0248*, JRAU

APG III Family	**All plants recorded on Island (2010 & 2011)**	**2010 CSIR Inventory**	**2010- 2011 BS Inventory**	**I/N/G/O**	**Voucher**
Asteraceae	*Oncosiphon sabulosum* (Wolley-Dod) Källersjö	R	N/R	N	—
Asteraceae	*Oncosiphon suffruticosum* (L.) Källersjö	N/R	R	N	*BS0054*, JRAU
Asteraceae	*Pseudognaphalium luteoalbum* (L.) Hilliard & B.L.Burtt	N/R	R	N	*BS0262*, JRAU
Asteraceae	*Senecio angulatus* L.f.	R	N/R	N	—
Asteraceae	*Senecio elegans* L.	R	N/R	N	—
Asteraceae	*Senecio maritimus* L.f.	R	R	N	*BS0078*, JRAU
Asteraceae	*Sonchus* sp.1	N/R	R	N	*BS0257*, JRAU
Basellaceae	*Anredera cordifolia* (Ten.) Steenis	R	N/R	N	—
Boraginaceae	*Amsinckia menziesii* (Lehm.) A.Nelson & J.F.Macbr.	N/R	R	O	*BS0290*, JRAU
Boraginaceae	*Echium vulgare* L.	N/R	R	I	*BS0289*, JRAU
Brassicaceae	Brassicaceae Indet.1	N/R	R	O	*BS0065*, JRAU
Brassicaceae	*Lepidium didymum* L.	R	N/R	I	—
Brassicaceae	*Rapistrum rugosum* (L.) All.	N/R	R	I	*BS0263*, JRAU
Cactaceae	*Epiphyllum phyllanthus* (L.) Haw.	R	N/R	I	—
Cactaceae	*Opuntia stricta* (Haw.) Haw.	N/R	R	I	*BS0106*, JRAU
Campanulaceae	*Wahlenbergia androsacea* A.DC.	R	N/R	G	—
Caryophyllaceae	*Dianthus caryophyllus* L.	N/R	R	I	*BS0152*,

APG III Family	**All plants recorded on Island (2010 & 2011)**	**2010 CSIR Inventory**	**2010- 2011 BS Inventory**	**I/N/G/O**	**Voucher**
					JRAU
Caryophyllaceae	*Polycarpon tetraphyllum* (L.) L.	N/R	R	N	*BS0134*, JRAU
Caryophyllaceae	*Sagina saginoides* (L.) H.Karst	N/R	R	O	*BS0258*, JRAU
Caryophyllaceae	*Silene cretica* L.	N/R	R	I	*BS0278*, JRAU
Caryophyllaceae	*Spergularia media* (L.) C.Presl	R	N/R	N	—
Casuarinaceae	*Casuarina cunninghamiana* Miq.	R	N/R	I	—
Celastraceae	*Catha edulis* (Vahl) Endl.	N/R	R	I	*BS0153*, JRAU
Colchicaceae	*Ornithoglossum dinteri* K.Krause	R	N/R	N	—
Colchicaceae	*Ornithoglossum* sp.1	N/R	R	N	*BS0280*, JRAU
Colchicaceae	*Ornithoglossum viride* (L.f.) Dryand. ex W.T.Aiton	R	R	N	*BS0243*, JRAU
Combretaceae	*Combretum kraussii* Hochst.	N/R	R	O	*BS0095*, JRAU
Convovulaceae	*Ipomoea mauritiana* Jacq.	R	N/R	N	—
Crassulaceae	*Aeonium spathulatum* (Hornem.) Praeger	R	N/R	N	—
Crassulaceae	*Cotyledon orbiculata* L.	N/R	R	N	*BS0129*, JRAU
Crassulaceae	*Crassula decumbens* Thunb.	R	N/R	G	—
Crassulaceae	*Crassula multicava* Lem.	N/R	R	O	*BS0083*, JRAU
Crassulaceae	*Crassula natans* Thunb.	R	N/R	N	—

APG III Family	All plants recorded on Island (2010 & 2011)	2010 CSIR Inventory	2010- 2011 BS Inventory	I/N/G/O	Voucher
Crassulaceae	*Crassula ovata* (Mill.) Druce	R	N/R	N	—
Crassulaceae	*Crassula thunbergiana* Schult.	R	N/R	N	—
Crassulaceae	*Crassula umbellata* Thunb.	R	N/R	N	—
Crassulaceae	*Crassula vaillantii* (Willd.) Roth	R	N/R	N	—
Crassulaceae	*Kalanchoe beharensis* Drake	N/R	R	G	*BS0119*, JRAU
Cucurbitaceae	*Citrullus lanatus* (Thunb.) Matsum. & Nakai	R	N/R	N	—
Cucurbitaceae	*Cucumis africanus* L.f.	R	N/R	G	—
Cucurbitaceae	*Cucumis anguria* L.	R	R	O	*BS0150*, JRAU
Cucurbitaceae	*Cucumis myriocarpus* Naudin	R	N/R	N	—
Cupressaceae	*Cupressus macrocarpa* Hartw.	N/R	R	I	*BS0070*, JRAU
Cupressaceae	*Cupressus sempervirens* L.	R	N/R	I	—
Cyperaceae	*Cyperus textilis* Thunb.	N/R	R	N	*BS0096*, JRAU
Cyperaceae	*Isolepis antarctica* (L.) Roem. & Schult.	R	N/R	N	—
Cyperaceae	*Isolepis incomtula* Nees	R	N/R	N	—
Draceanaceae	*Draceana draco* (L.) L.	R	N/R	I	—
Ebenaceae	*Euclea racemosa* L.	N/R	R	N	*BS0073*, JRAU
Euphorbiaceae	*Euphorbia drummondii* Boiss.	N/R	R	I	*BS0157*, JRAU
Euphorbiaceae	*Euphorbia peplus* L.	N/R	R	I	*BS0149*, JRAU
Euphorbiaceae	*Euphorbia polygona* Haw.	R	N/R	N	—

APG III Family	**All plants recorded on Island (2010 & 2011)**	**2010 CSIR Inventory**	**2010- 2011 BS Inventory**	**I/N/G/O**	**Voucher**
Euphorbiaceae	*Ricinus communis* L.	N/R	R	I	*BS0267*, JRAU
Fabaceae	*Acacia cyclops* G.Don	N/R	R	I	*BS0068*, JRAU
Fabaceae	*Ceratonia siliqua* L.	R	N/R	I	—
Fabaceae	*Crotalaria capensis* Jacq.	R	N/R	N	—
Fabaceae	*Erythrina caffra* Thunb.	N/R	R	N	*BS0057*, JRAU
Fabaceae	*Medicago arabica* (L.) Huds.	R	R	I	*BS0285*, JRAU
Fabaceae	*Medicago polymorpha* L.	R	N/R	G	—
Fabaceae	*Psoralea repens* P.J.Bergius	R	N/Rt	N	—
Fabaceae	*Trifolium tomentosum* L.	N/R	R	I	*BS0260*, JRAU
Flacourtiaceae	*Dovyalis caffra* (Hook. f. & Harv.) Warb.	N/R	R	N	*BS0094*, JRAU
Frankeniaceae	*Frankenia pulverulenta* L.	R	N/R	I	—
Fumariaceae	*Cysticapnos vesicaria* (L.) Fedde	R	N/R	N	—
Geraniaceae	*Erodium moschatum* (L.) L'Hér.	N/R	R	I	*BS0245*, JRAU
Geraniaceae	*Geranium incanum* Burm.f.	N/R	R	O	*BS0109*, JRAU
Geraniaceae	*Geranium molle* L.	N/R	R	I	*BS0147*, JRAU
Geraniaceae	*Pelargonium capitatum* (L.) L'Hér.	N/R	R	N	*BS0168*, JRAU

APG III Family	All plants recorded on Island (2010 & 2011)	2010 CSIR Inventory	2010- 2011 BS Inventory	I/N/G/O	Voucher
Geraniaceae	*Pelargonium cucullatum* subsp. *tabulare* Volschenk	N/R	R	N	*BS0111*, JRAU
Hycinthaceae	*Albuca fragrans* Jacq.	R	N/R	G	—
Iridaceae	*Ferraria crispa* Burm.	N/R	R	N	*BS0255*, JRAU
Iridaceae	*Moraea collina* Thunb.	R	N/R	N	—
Iridaceae	*Moraea setifolia* (L.f.) Druce	R	N/R	N	—
Iridaceae	*Romulea rosea* (L.) Eckl.	N/R	R	N	*BS0249*, JRAU
Iridaceae	*Romulea obscura* Klatt	N/R	R	N	*BS0281*, JRAU
Lamiaceae	*Ballota africana* (L.) Benth.	N/R	R	N	*BS0288*, JRAU
Lamiaceae	*Leonotis leonurus* (L.) R.Br.	N/R	R	N	*BS0055*, JRAU
Lamiaceae	*Salvia lanceolata* Lam.	N/R	R	N	*BS0110*, JRAU
Lessionaceae	Lessionaceae sp.1	N/R	R	O	*BS0264*, JRAU
Malvaceae	*Grewia occidentalis* L.	R	N/R	N	—
Malvaceae	*Hibiscus rosa-sinensis* L.	N/R	R	I	*BS0104*, JRAU
Malvaceae	*Lagunaria patersonia* (Andrews) G. Don	N/R	R	I	*BS0107*, JRAU
Malvaceae	*Malva arborea* (L.) Webb & Berthel.	R	N/R	G	—
Malvaceae	*Malva neglecta* Wallr.	N/R	R	I	*BS0155*,

APG III Family	All plants recorded on Island (2010 & 2011)	2010 CSIR Inventory	2010- 2011 BS Inventory	I/N/G/O	Voucher
					JRAU
Malvaceae	*Malva parviflora* L.	N/R	R	I	*BS0092*, JRAU
Malvaceae	*Malva* sp.1	R	N/R	I	
Menispermaceae	*Cissampelos capensis* L.f.	N/R	R	N	*BS0074*, JRAU
Molluginaceae	*Pharnaceum subtile* E.Mey. ex Fenzl	R	N/R	N	—
Moraceae	*Ficus carica* L.	N/R	R	I	*BS0084*, JRAU
Moraceae	*Ficus microcarpa* L.f.	N/R	R	I	*BS0077*, JRAU
Moraceae	*Morus alba* L.	N/R	R	I	*BS0124*, JRAU
Myrtaceae	*Callistemon viminalis* (Sol. ex Gaertn.) G.Don ex Loudon	N/R	R	I	*BS0118*, JRAU
Myrtaceae	*Corymbia gummifera* (Gaertn.) K.D.Hill & L.A.S.Johnson	R	N/R	I	—
Myrtaceae	*Eucalyptus cladocalyx* F.Muell.	R	N/R	I	—
Myrtaceae	*Eucalyptus globulus* Labill.	N/R	R	I	*BS0159*, JRAU
Myrtaceae	*Eucalyptus lehmannii* (Schauer) Benth.	R	N/R	I	—
Myrtaceae	*Eucalyptus* sp.1	N/R	R	I	*BS0063*, JRAU
Myrtaceae	*Eucalyptus* sp.2	N/R	R	I	*BS0079*, JRAU
Myrtaceae	*Eucalyptus* sp.3	N/R	R	I	*BS0130*,

APG III Family	**All plants recorded on Island (2010 & 2011)**	**2010 CSIR Inventory**	**2010- 2011 BS Inventory**	**I/N/G/O**	**Voucher**
					JRAU
Myrtaceae	*Eucalyptus sp.*4	N/R	R	I	*BS0242*, JRAU
Myrtaceae	*Leptospermum laevigatum* (Gaertn.) F.Muell.	N/R	R	I	*BS0158*, JRAU
Myrtaceae	*Melaleuca bracteata* F.Muell.	R	N/R	I	—
Myrtaceae	*Metrosideros excelsa* Sol. ex Gaertn.	N/R	R	I	*BS0097*, JRAU
Myrtaceae	*Syzygium cordatum* Hochst. ex Krauss	R	N/R	N	—
Nyctaginaceae	*Bougainvillea glabra* Choisy	N/R	R	I	*BS0108*, JRAU
Nyctaginaceae	*Mirabilis jalapa* L.	N/R	R	I	*BS0088*, JRAU
Oleaceae	*Ligustrum lucidum* W.T.Aiton	N/R	R	I	*BS0102*, JRAU
Oleaceae	*Olea europaea* subsp. *cuspidata* (Wall. & G.Don) Cif.	N/R	R	N	*BS0123*, JRAU
Oleaceae	Oleaceae Indet.1	N/R	R	I	*BS0146*, JRAU
Orchidaceae	*Satyrium odorum* Sond.	R	N/R	I	—
Orobanchaceae	*Paliavana racemosa* (Vell.) Fritsch	R	N/R	I	—
Oxalidaceae	*Oxalis corniculata* L.	R	N/R	N	—
Oxalidaceae	*Oxalis pes-caprae* L.	N/R	R	I	*BS0251*, JRAU
Phytollacaceae	*Phytolacca dioica* L.	R	N/R	I	—
Pinaceae	*Pinus halepensis* Mill.	N/R	R	I	*BS0081*,

APG III Family	All plants recorded on Island (2010 & 2011)	2010 CSIR Inventory	2010- 2011 BS Inventory	I/N/G/O	Voucher
					JRAU
Pinaceae	*Pinus radiata* D.Don	N/R	R	I	*BS0056*, JRAU
Pittisporaceae	*Pittosporum* sp.1	R	N/R	I	—
Plantaginaceae	*Plantago coronopus* L.	R	N/R	I	—
Plumbaginaceae	*Plumbago auriculata* Lam.	R	N/R	G	—
Poaceae	*Agrostis* sp.1	R	N/R	N	—
Poaceae	*Ammophila arenaria* (L.) Link	N/R	R	I	*BS0231*, JRAU
Poaceae	*Arundo donax* L.	N/R	R	I	*BS0142*, JRAU
Poaceae	*Avena barbata* Pott ex Link	R	N/R	I	—
Poaceae	*Avena sativa* L.	N/R	R	I	*BS0080*, JRAU
Poaceae	*Bromus catharticus* Vahl	N/R	R	I	*BS0292*, JRAU
Poaceae	*Bromus diandrus* Roth	N/R	R	I	*BS0273*, JRAU
Poaceae	*Bromus japonicus* Thunb.	R	N/R	I	—
Poaceae	*Cynodon dactylon* (L.) Pers.	N/R	R	N	*BS0132*, JRAU
Poaceae	*Ehrharta brevifolia* Schrad.	R	N/R	N	—
Poaceae	*Ehrharta longiflora* Sm.	R	N/R	N	—
Poaceae	*Ehrharta villosa* Schult.f.	R	N/R	N	—
Poaceae	*Elymus distichus* (Thunb.) Melderis	R	N/R	N	—
Poaceae	*Fingerhuthia africana* Lehm.	R	N/R	I	—

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Poaceae	*Hordeum murinum* L.	R	N/R	I	—
Poaceae	*Lagurus ovatus* L.	R	N/R	I	—
Poaceae	*Lolium temulentum* L.	R	N/R	I	—
Poaceae	*Pennisetum clandestinum* Hochst. ex Chiov.	R	N/R	I	—
Poaceae	*Pennisetum villosum* Fresen.	R	N/R	I	—
Poaceae	*Phalaris minor* Retz.	R	N/R	I	—
Poaceae	*Poa annua* L.	R	N/R	I	—
Poaceae	Poaceae sp.1	N/R	R	O	*BS0232*, JRAU
Poaceae	Poaceae sp.2	N/R	R	O	*BS0236*, JRAU
Poaceae	*Sporobolus virginicus* (L.) Kunth	R	N/R	N	—
Polygalaceae	*Muraltia satureioides* Burch. ex DC.	N/R	R	I	*BS0163*, JRAU
Polygalaceae	*Muraltia spinosa* (L.) F.Forest & J.C.Manning	N/R	R	I	*BS0164*, JRAU
Polygalaceae	*Polygala myrtifolia* L.	N/R	R	G	*BS0165*, JRAU
Polygonaceae	*Emex australis* Steinh.	R	N/R	I	—
Polygonaceae	Indet.	N/R	R	I	*BS0244*, JRAU
Polygonaceae	Polygonaceae sp.1	N/R	R	G	*BS0268*, JRAU
Portulacaceae	*Portulaca oleracea* L.	R	N/R	I	—
Portulacaceae	*Portulacaria afra* Jacq.	N/R	R	N	*BS0169*, JRAU

APG III Family	All plants recorded on Island (2010 & 2011)	2010 CSIR Inventory	2010- 2011 BS Inventory	I/N/G/O	Voucher
Primulaceae	*Anagallis arvensis* L.	N/R	R	I	*BS0283*, JRAU
Primulaceae	*Anagallis* sp.1	N/R	R	I	*BS0284*, JRAU
Restionaceae	*Chondropetalum tectorum* (L.f.) Raf.	N/R	R	O	*BS0151*, JRAU
Restionaceae	*Thamnochortus spicigerus* (Thunb.) Spreng.	N/R	R	I	*BS0171*, JRAU
Rosaceae	*Prunus armeniaca* L.	R	N/R	I	—
Sapotaceae	*Sideroxylon inerme* L.	N/R	R	N	*BS0117*, JRAU
Saxifragaceae	Saxifragaceae sp.1	N/R	R	O	*BS0228*, JRAU
Scrophulariaceae	*Hemimeris racemosa* (Houtt.) Merr.	R	N/R	N	—
Scrophulariaceae	*Myoporum cf laetum* G.Forst.	N/R	R	I	*BS0122*, JRAU
Scrophulariaceae	*Myoporum laetum* G. Forst.	N/R	R	I	*BS0060*, JRAU
Scrophulariaceae	*Phyllopodium capillare* (L.f.) Hilliard	R	N/R	N	—
Scrophulariaceae	*Zaluzianskya villosa* F.W. Schmidt	N/R	R	N	*BS0247*, JRAU
Solanaceae	*Datura stramonium* L.	N/R	R	I	*BS0089*, JRAU
Solanaceae	*Lycium afrum* L.	N/R	R	N	*BS0140*, JRAU
Solanaceae	*Lycium ferocissimum* Miers	N/R	R	N	*BS0069*,

APG III Family	All plants recorded on Island (2010 & 2011)	2010 CSIR Inventory	2010- 2011 BS Inventory	I/N/G/O	Voucher
					JRAU
Solanaceae	*Lycopersicon esculentum* Mill.	N/R	R	I	*BS0156*, JRAU
Solanaceae	*Nicotiana glauca* Graham	N/R	R	I	*BS0101*, JRAU
Solanaceae	*Physalis peruviana* L.	N/R	R	I	*BS0237*, JRAU
Solanaceae	*Solanum africanum* Mill.	R	N/R	N	—
Solanaceae	*Solanum anguivi* Lam.	R	N/R	N	—
Solanaceae	*Solanum guineense* (L.) Mill.	N/R	R	O	*BS0265*, JRAU
Solanaceae	*Solanum linnaeanum* Hepper & P.-M.L.Jaeger	N/R	R	N	*BS0143*, JRAU
Solanaceae	*Solanum nigrum* L.	N/R	R	I	*BS0100*, JRAU
Strelitziaceae	*Strelitzia reginae* Banks ex Aiton	N/R	R	G	*BS0271*, JRAU
Tamaricaceae	*Tamarix chinensis* Lour.	N/R	R	I	*BS0105*, JRAU
Tecophilaeaceae	*Cyanella orchidiformis* Jacq.	N/R	R	N	*BS0261*, JRAU
Tropaeolaceae	*Tropaeolum majus* L.	N/R	R	I	*BS0282*, JRAU
Urticaceae	*Didymodoxa capensis* (L.f.) Friis & Wilmot-Dear	R	N/R	N	—
Urticaceae	*Urtica urens* L.	N/R	R	I	*BS0062*, JRAU

APG III Family	All plants recorded on Island (2010 & 2011)	2010 CSIR Inventory	2010- 2011 BS Inventory	I/N/G/O	Voucher
Vitaceae	*Vitis vinifera* L.	R	N/R	G	—
Xanthorrheaceae	*Phormium tenax* J.R.Forst. & G.Forst.	N/R	R	I	*BS0141*, JRAU
Xanthorrheaceae	*Aloe arborescens* Mill.	N/R	R	N	*BS0270*, JRAU
Xanthorrheaceae	*Aloe barberae* Dyer	R	N/R	G	—
Xanthorrheaceae	*Aloe camperi* Schweinf.	R	N/R	G	—
Xanthorrheaceae	*Aloe ferox* Mill.	R	N/R	G	—
Xanthorrheaceae	*Aloe maculata* All.	N/R	R	N	*BS0145*, JRAU
Xanthorrheaceae	*Aloe thraskii* Baker	R	N/R	G	—
Xanthorrheaceae	*Gasteria* sp.1	R	N/R	G	—
Xanthorrheaceae	*Trachyandra ciliata* (L.f.) Kunth	N/R	R	N	*BS0256*, JRAU
Xanthorrheaceae	*Trachyandra divaricata* (Jacq.) Kunth	N/R	R	N	*BS0091*, JRAU
Xanthorrheaceae	*Trachyandra* sp.1	R	N/R	N	—
Zygophyllaceae	Zygophyllaceae Indet.1	N/R	R	O	*BS0061*, JRAU

I designed a series of study plots across the island (Figure 2.9). The entire island was divided into 2,401 plots of 50m x 50m. In total, 147 of these plots were selected for this survey using a “random number generating sequence” technique (www.random.org). This random technique was applied to avoid bias in plot distribution within vegetation and habitat types. I excluded 20 plots that fell in gardens, buildings, the ocean or bird nesting sites. In total 127 plots falling in accessible areas were considered for data collection and, in these plots, we recorded species presence/absence and collected tissue samples in silica gel for DNA extraction.

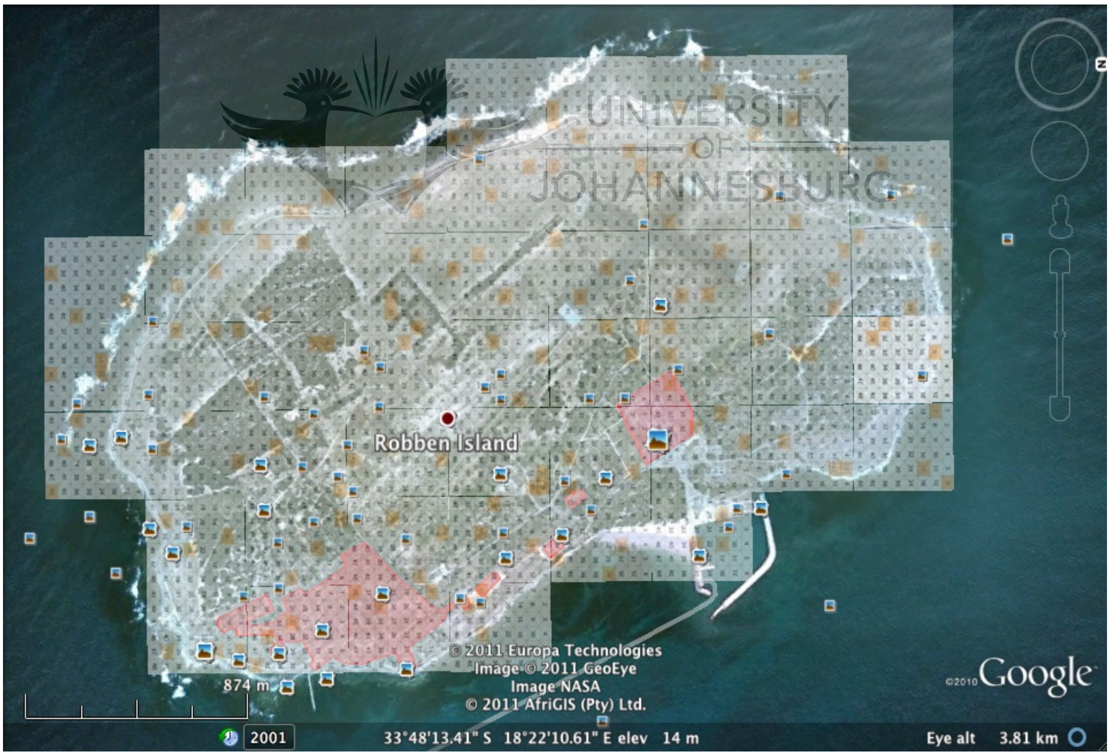


Figure 2.9. Map indicating the random distribution of plots on the island (in brown). Shaded areas (in red) specify buildings and gardens.

2.3.1. PHYLOGENETIC RECONSTRUCTION

Plant tissue was extracted using the 10 × CTAB protocol of Doyle & Doyle (1987). Plant barcoding loci (that is, a portion of the plastid *matK* gene and the subunit 'a' of *rbcL*) were amplified and sequenced (123 *rbcLa* and 119 *matK* sequences) following protocols described by the CBOL Plant Working Group (2009). Due to sequencing failure for some species, we downloaded additional sequences from GenBank (11 *rbcLa* and 15 *matK*). Thirty-six species were excluded from the matrix due to lack of DNA sequence data (Table 2.1). DNA sequences were aligned manually in PAUP* (version 4.0b.10; Swofford 2002). The matrix consisted of 133 taxa, representing 68 natives, and 65 invasive species.

I reconstructed the phylogenetic tree of the island's flora using the Bayesian approach implemented in BEAST 1.5.3 (Drummond & Rambaut 2007), which allows simultaneous estimation of the topology, substitution rates and node ages (Drummond & Rambaut 2007). I defined two data partitions according to the DNA regions used in the study (*rbcLa* and *matK*). I implemented the GTR + I + G model of sequence evolution for each partition, chosen based on the Akaike information Criterion scores for substitution models evaluated using jModeltest 0.1.1 (Posada 2008). A speciation model following a Yule process was selected for the tree prior, with an uncorrelated lognormal clock model allowing rate variation among branches. The age of the root node of eudicots (126 mya; Crane, Frils & Pedersen 1995) was used as calibration point to constrain the root of the tree, implemented as a normally distributed prior (mean 126 mya, standard deviation 1). Metropolis coupled Monte Carlo Markov Chains were run for 20 million generations, sampling every 2000th generation. Convergence was assessed using Tracer 1.5 (Rambaut & Drummond 2007), the Effective Sample Size for all estimated parameters was greater than 200. Of the 10,001 posterior trees I obtained, the first 1,000 were discarded as 'burn-in' before combining all runs to build the maximum clade credibility tree using TreeAnnotator 1.5.1 (Drummond & Rambaut 2007). *Amborella trichopoda* was used as outgroup (APG III 2009)

2.3.2. DATA ANALYSES

The analyses followed five steps. Firstly, I calculated the phylogenetic distance of each invasive to its nearest native neighbour on the entire phylogeny ($PNND_{Inv-Nat}$), which I compared to the nearest neighbour distances of each native to native ($PNND_{Nat-Nat}$) and invasive to invasive ($PNND_{Inv-Inv}$). The PNND values were computed using Phylocom 4.1 (Webb, Ackerley & Kembel 2008). I referred to these distances as island-scale distances, since they were calculated based on the entire phylogenetic tree.

Secondly, I conducted similar analysis at the plot scale. I calculated the mean PNND for the subtrees of each plot, thereby evaluating whether the patterns at island scale, if any, were present at a more local scale where competition might be expected to be more intense.

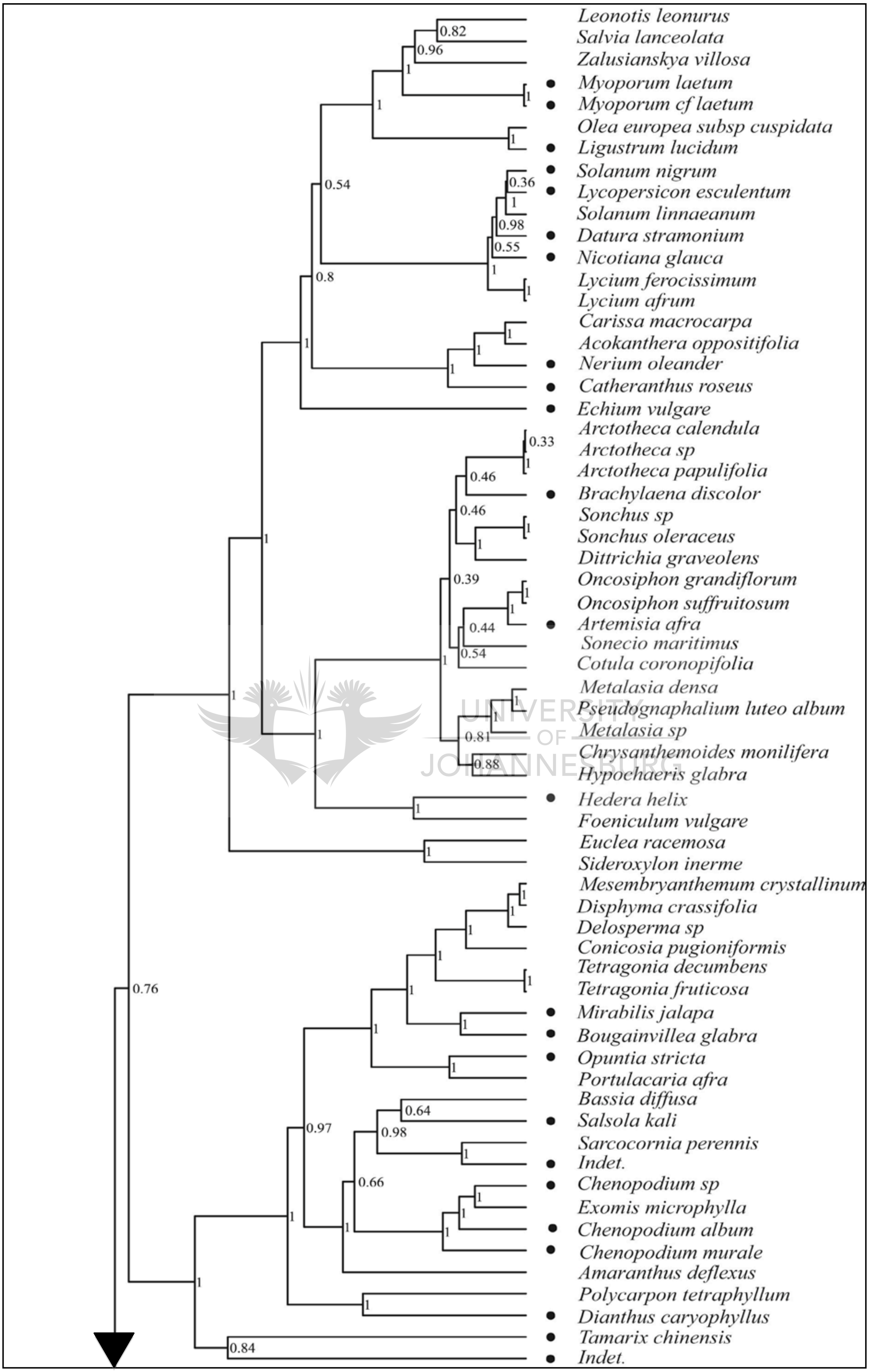
Thirdly, I calculated the mean phylogenetic distances (MPD) of invasives to natives, natives to natives and invasives to invasives within the 127 plots. This analysis is complementary to the previous ones, as MPD evaluates the mean pairwise distance between all species co-occurring within plots, and not just the distance between a species and its nearest neighbour as in PNND (Webb, Ackerly & Webb 2008). MPD was calculated in Phylocom

4.1. (Webb, Ackerley & Webb 2008). All significance tests were assessed using a two-sample t-test.

I further investigated whether the patterns observed based on PNND and MPD analyses were generated due to chance alone. This was assessed by bootstrapping (sampling with replacement) the PNND and MPD values 10,000 times to obtain a 95% confidence interval for the mean of both metrics. Finally, I assessed whether the patterns observed were scale-dependent. I therefore conducted a two-way ANOVA using the PNND as response variable, with scale (island vs. plot) and a distance category (invasive-native, native-native, invasive-invasive) as categorical explanatory variables. All statistical analyses, unless otherwise stated, were conducted in R 2.14.1 (R Development Core Team 2011).

2.4. Results

The phylogenetic tree of all 134 species (133 collected + *Amborella trichopoda*) was in broad agreement with the latest phylogenetic studies of angiosperms (APG III 2009; Figure 2.9). Also, the ages of the nodes were in agreement with previous dating of large-scale phylogenetic trees (Wikström, Savolainen & Chase 2001; Davies et al. 2011; Figure 2.10).


Leonotis leonurus
Salvia lanceolata
Zalusianskya villosa
● Myoporum laetum
● Myoporum cf laetum
Olea europea subsp cuspidata
● Ligustrum lucidum
● Solanum nigrum
● Lycopersicon esculentum
Solanum linnaeanum
● Datura stramonium
● Nicotiana glauca
Lycium ferocissimum
Lycium afrum
Carissa macrocarpa
Acokanthera oppositifolia
● Nerium oleander
● Catheranthus roseus
● Echium vulgare
Arctotheca calendula
Arctotheca sp
Arctotheca papulifolia
● Brachylaena discolor
Sonchus sp
Sonchus oleraceus
Dittrichia graveolens
Oncosiphon grandiflorum
Oncosiphon suffruitosum
● Artemisia afra
Sonecio maritimus
Cotula coronopifolia
Metalasia densa
Pseudognaphalium luteo album
Metalasia sp
Chrysanthemoides monilifera
Hypochaeris glabra
● Hedera helix
Foeniculum vulgare
Euclea racemosa
Sideroxylon inerme
Mesembryanthemum crystallinum
Disphyma crassifolia
Delosperma sp
Conicosia pugioniformis
Tetragonia decumbens
Tetragonia fruticosa
● Mirabilis jalapa
● Bougainvillea glabra
● Opuntia stricta
Portulacaria afra
Bassia diffusa
● Salsola kali
Sarcocornia perennis
● Indet.
● Chenopodium sp
Exomis microphylla
● Chenopodium album
● Chenopodium murale
Amaranthus deflexus
Polycarpon tetraphyllum
● Dianthus caryophyllus
● Tamarix chinensis
● Indet.
0.82
0.96
1
1
1
1
0.54
0.36
1
0.98
0.55
1
0.8
1
1
1
1
1
0.33
1
0.46
0.46
1
1
0.39
1
1
0.44
0.54
1
1
1
1
0.81
0.88
1
1
1
1
1
1
1
1
0.76
1
1
1
0.64
0.97
0.98
1
0.66
1
1
1
1
1
1
0.84

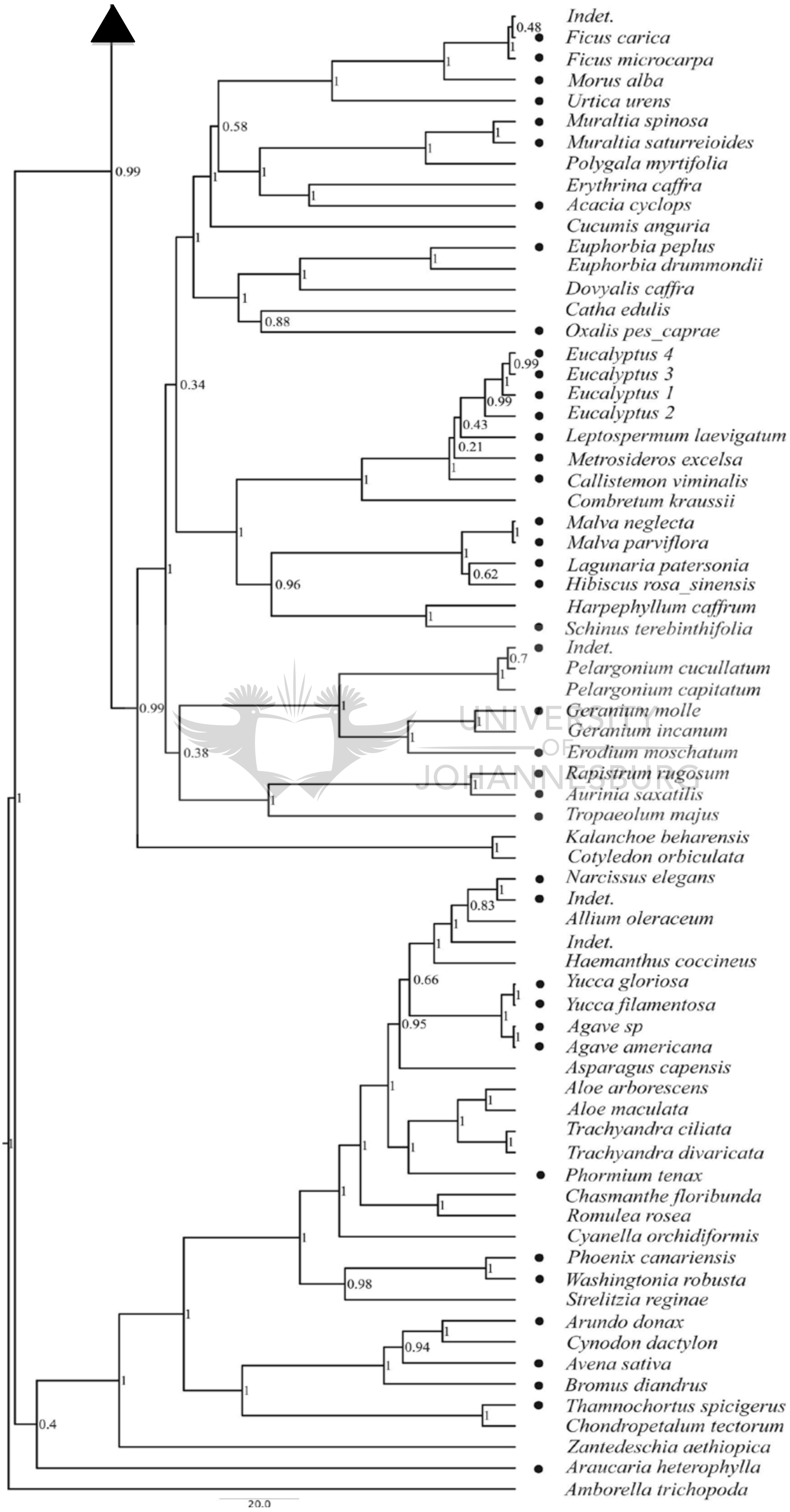

Indet.
Ficus carica
Ficus microcarpa
Morus alba
Urtica urens
Muraltia spinosa
Muraltia saturreioides
Polygala myrtifolia
Erythrina caffra
Acacia cyclops
Cucumis anguria
Euphorbia peplus
Euphorbia drummondii
Dovyalis caffra
Catha edulis
Oxalis pes_caprae
Eucalyptus 4
Eucalyptus 3
Eucalyptus 1
Eucalyptus 2
Leptospermum laevigatum
Metrosideros excelsa
Callistemon viminalis
Combretum kraussii
Malva neglecta
Malva parviflora
Lagunaria patersonia
Hibiscus rosa_sinensis
Harpephyllum caffrum
Schinus terebinthifolia
Indet.
Pelargonium cucullatum
Pelargonium capitatum
Geranium molle
Geranium incanum
Erodium moschatum
Rapistrum rugosum
Aurinia saxatilis
Tropaeolum majus
Kalanchoe beharensis
Cotyledon orbiculata
Narcissus elegans
Indet.
Allium oleraceum
Indet.
Haemanthus coccineus
Yucca gloriosa
Yucca filamentosa
Agave sp
Agave americana
Asparagus capensis
Aloe arborescens
Aloe maculata
Trachyandra ciliata
Trachyandra divaricata
Phormium tenax
Chasmanthe floribunda
Romulea rosea
Cyanella orchidiformis
Phoenix canariensis
Washingtonia robusta
Strelitzia reginae
Arundo donax
Cynodon dactylon
Avena sativa
Bromus diandrus
Thamnochortus spicigerus
Chondropetalum tectorum
Zantedeschia aethiopica
Araucaria heterophylla
Amborella trichopoda
0.48
1
1
1
0.58
1
1
1
1
1
1
1
1
0.88
0.99
0.99
1
0.99
0.43
0.21
1
1
0.34
1
1
1
0.62
0.96
1
0.99
0.7
1
1
1
1
0.38
1
1
1
1
1
0.83
1
1
0.66
1
1
1
1
0.95
1
1
1
1
1
1
1
1
1
1
0.98
1
0.94
1
1
1
1
1
0.4
1
20.0

Figure 2.10. Phylogenetic tree of the flora of Robben Island, except *Amborella trichopoda*, which is used as outgroup (Pages 52 and 53). Values indicate posterior probabilities for each node. Dots indicate invasive plants on the island.

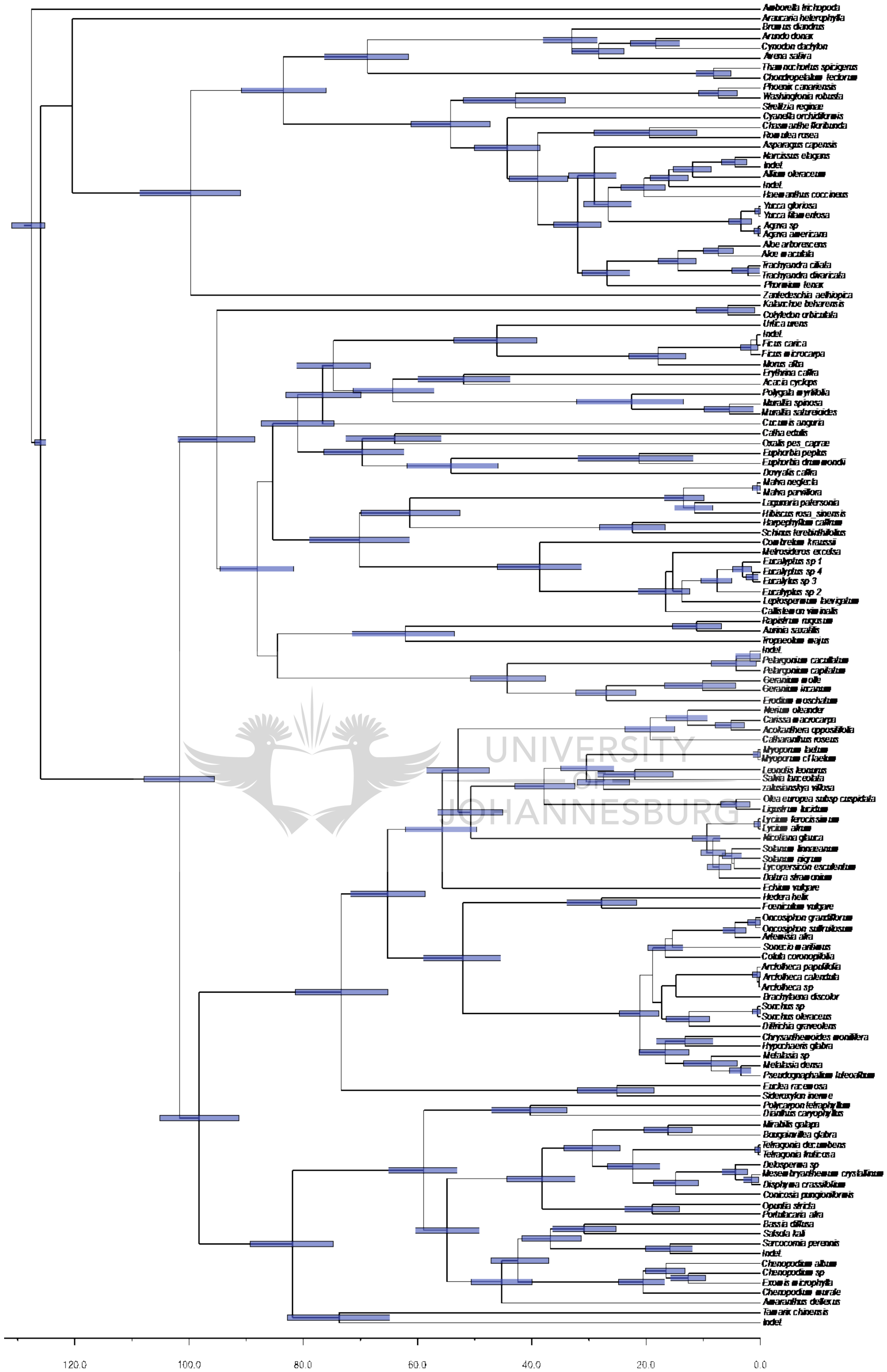


Figure 2.11. Chronogram with scale indicating node ages (in million years) at the bottom and blue bars representing 95% confidence intervals for node ages.

Darwin’s naturalisation hypothesis suggests that alien species will be successfully established in a novel environment only if they are less related to native species. Therefore, I predicted that the phylogenetic distance between native and invasive should be higher than that between natives. At the island scale, i.e. using the entire phylogenetic tree, I found that the mean PNND between invasives and natives (81.88 million years; my) was higher than that between invasives (50.90 my) or natives (47.99 my; p = 0.00003 and p = 0.00006, respectively; (Figure 2.11). In contrast, PNND between natives was not significantly different from that between invasives (p = 0.75).

At the plot scale, we found a similar pattern, i.e. the mean PNNDs between invasives and natives (180.07 my) was larger than that between invasives (158.20 my; p < 0.0001) and between natives (87.61 my; p < 0.0001; (Figure 2.11). In addition, PNND between natives was significantly lower than that between invasives (p < 0.0001; Figure 2.11).

Further, results for the MPD metric at the plot scale were consistent with those from the PNND analyses: MPD of invasives to natives was larger than that between natives (216.93 versus 193.39 my; p < 0.0001) and between invasives (216.93 versus 192.62 my; p < 0.0001; Figure 2.11). MPD between natives and between invasives were not significantly different (p = 0.75; Figure 2.11).

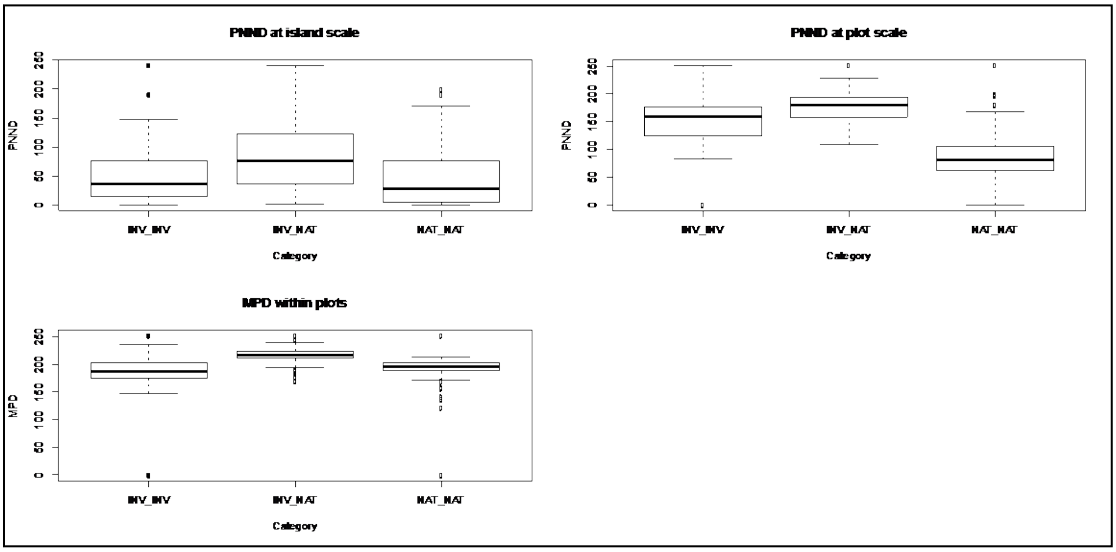


Figure 2.12. Boxplots of phylogenetic nearest neighbor distances (PNND), at island scale, PNND at plot scale and mean phylogenetic distance (MPD), in million years on Robben Island for each pair of native-invasive (Nat_Inv) plants compared to each native-native (Nat_Nat) pair and invasive-invasive (Inv_Inv) pair. The boxes show the first and third quartiles, the median is shown by the horizontal bold line, the range of the data by the dashed line, and the outliers by circles.

These patterns of PNND and MPD could be due to chance alone. Therefore, we conducted a bootstrapping analysis, which shows that the higher value of invasive-native distances is significant ($p<0.05$; red line; Figure 2.13).

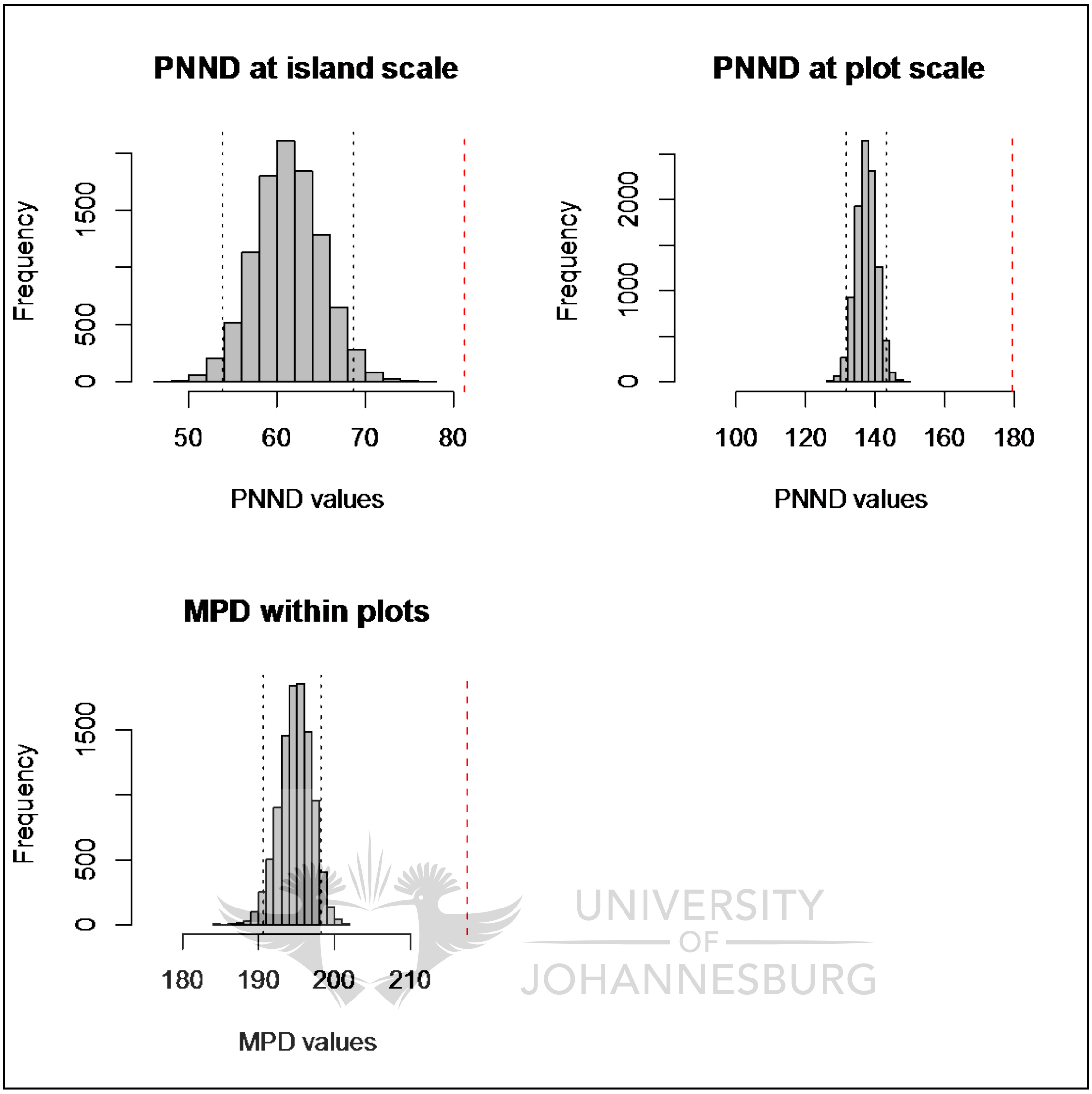


Figure 2.13. Bootstrapping analysis to demonstrate the effect of Chance on the longer distances between Invasives and Natives is significant (p<0.05; red line).

Finally, the test for possible scale-dependency shows that: (1) at both small and large scales, PNND between invasives and natives was always longer than that of natives to natives or invasives to invasives, and; (2) PNND between invasives and natives is significantly longer at the plot rather than the island scale (two-way ANOVA, F = 177.2, p < 0.001; Figure 2.13; Table 2.3).

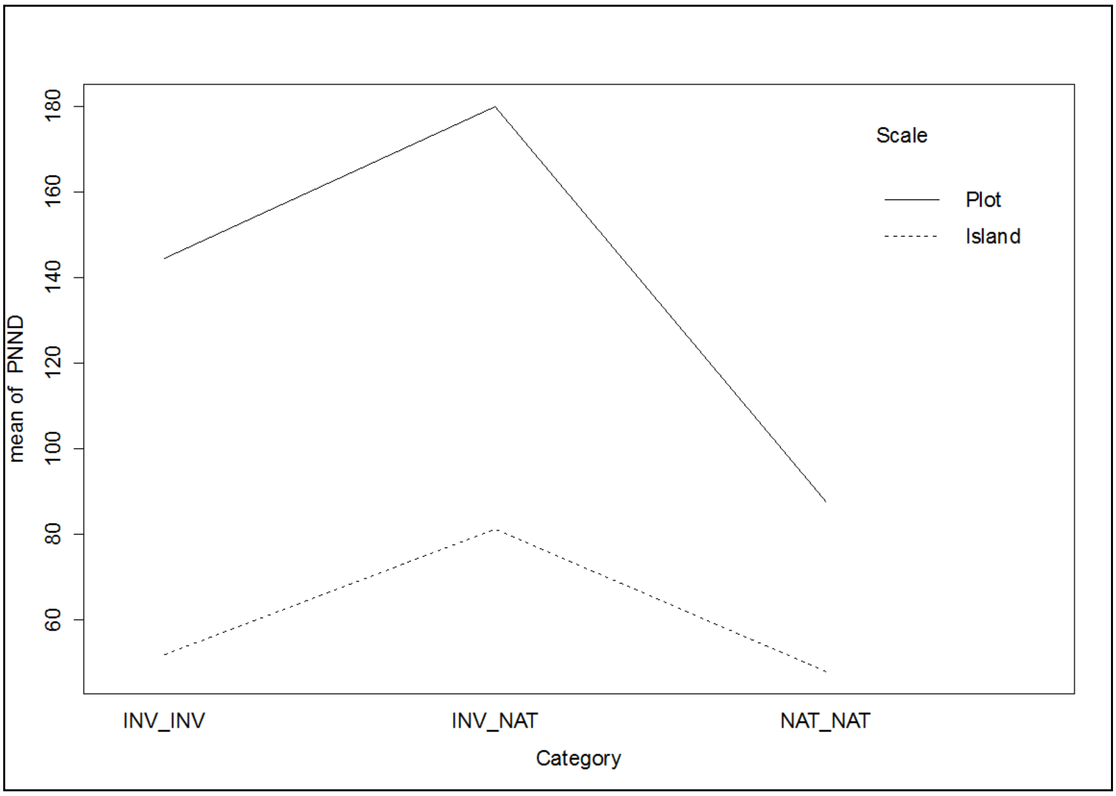


Figure 2.14.The effect of scale dependency at both small and large scales on the longer distances between natives and invasive.

Source	SS	d.f.	MS	F	p
Scale	779513	1	779513	335.50	< 0.001***
Category	507788	2	253894	109.28	< 0.001***
Residuals	1359195	585	2323		

Table 2.3. Two-way Anova showing the effect of scale on the longer distances between natives and invasive.

2.5. Discussion

The current, unprecedented rate of biodiversity loss is a matter of great concern among ecologists (Pimm et al. 1995; Mace, Masundire & Baillie 2005; Davies et al. 2011). To date, several drivers of biodiversity loss have been identified, with alien species being one of the most important factors (Holmes & Cowling 1997; Mack et al. 2000; Clavero & García-Berthou 2005; Sax & Gaines 2008; Winter et al. 2009; Schaefer et al. 2011). However, the underlying causes of invasiveness are still not fully understood, limiting our ability to predict which species become invasive (Maitner et al. 2011). Here, we examined the phylogenetic patterns of alien and native plants on Robben Island and evaluated whether these matched the predictions of Darwin’s naturalisation hypothesis.

Darwin’s hypothesis postulates that a new species is more likely to establish a sustained reproductive population in new ranges if there are no congeneric species in the recipient system (Darwin 1859). The rationale is that closely related species would be competing strongly for resources, thus limiting chances of co-occurring (Webb et al. 2002; see also reviews in Vamosi et al. 2009 and Cavender-Bares et al. 2009). Therefore, we predicted that species invading Robben Island should be phylogenetically less related to natives than natives are to each other. We found that the distance between invasive and native species on Robben Island is greater than that between natives, as predicted. Furthermore, the strength of this pattern is amplified within the local (plot) communities, where we would expect competition to be more intense (Lovette & Hochachka 2006; Swenson et al. 2006; Thuiller et al. 2010). This is a key finding, as it suggests that invaders at the local scale are selected from the islands species pool based, at least in part, on their evolutionary differences to the native community. This assertion is supported by the second metric we assessed, MPD, which concerns the relatedness of individual species relative to the entire native/invasive local community. Across the plots, each invasive species is more distantly related to the local native assemblage than each native is to the native community. This is an indication that the invasive species are occupying distinct niches, which were either vacant or previously occupied by natives that are now competitively excluded. These local scale findings certainly point to a role of Darwin's naturalisation hypothesis in shaping the composition of the island's flora, and the island scale findings are consistent with the expectations of this hypothesis. However, it is important to consider alternative explanations for the patterns observed as well as drawbacks of the approach, before accepting that Darwin's hypothesis applies at both the plot and island scales.

Defining a species as invasive, rather than just as an introduced species, and the magnitude of its invasion or invasive potential, is not a simple task and requires a great deal of ecological information. As a result, we adhered to Henderson (2007) and the opinions of local conservation authorities to determine which species were invasive on Robben Island. This includes species whose presence has been recorded recently on the island and which have subsequently colonised native habitats. It also includes plants brought to the island by humans or natural dispersal, which are known to be invasive in South Africa but which have not necessarily formed large invasive populations on the island. As such, some of these species may only be transient colonisers, or the populations may be maintained by ongoing dispersal from the mainland rather than by the establishment of self-sustaining, invasive populations. Our classification of invasive plants could, therefore, be biased; limiting the ability to predict which species might become truly invasive problems. However, the presence of each of the “invasive” species among native vegetation at the plot scale demonstrates that they are at the least, colonising native habitats in competition with native species.

Unfortunately, there is no detailed record of the nature and timing of introductions on the island. This is detrimental because, at the island scale, it does not allow us to definitively distinguish whether the non-random pattern of invasive species is due to competitive interactions (Darwin’s hypothesis) or due to the non-random introduction of species. Humans tend to introduce distantly related plants as ornamentals or for medicinal and agricultural purposes. This might lead to increased distances between our invasive and the native species. Blackburn & Duncan (2001) quantified the non-random introduction of birds using a global dataset. By analysing statistical distributions among different taxa and the location of introduction events, they showed that global introduction events of birds is not random and that species chosen for introduction tends to be abundant species which are easy to collect i.e. they were chosen based on specific traits valued by human (in plants this might include traits useful for horticulture, medicinal, adequacy for construction, food, etc.). Similarly, traits that might promote natural colonisation of the island by species introduced to South Africa, such as wind mediated seed dispersers that are often phylogenetically constrained. Although the introductions may not have been random, via humans or natural dispersal events, the Robben Island flora is small and close enough to the mainland that there are likely to have been random colonisations by large numbers of different species (relative to the island's community size) negating the biases of non-random introductions. In other words, despite some inevitable non-random introductions there are likely to have been sufficient random introductions to prevent this problem drastically shaping our results.

It is also likely that alien species distantly related to natives do not share the same natural enemies; their success on the island could therefore be linked to a release-from-enemies theory, providing opportunity for their population explosion (see Hill & Kotanen 2009). This could explain the pattern of relatedness between invasive and native species. Although not directly linked to competition for resources, as proposed by Darwin's naturalisation hypothesis, the pattern is still the result of a biological process dependent on the relatedness of invasive and native species. In escaping from enemies, these species gain a competitive edge over native species and, as such, we suggest that this is complementary to Darwin's hypothesis rather than an opposing theory.

Invasion success of aliens could also be favoured by some ecological traits that were not taken into account here, such as dispersal ability, habit or life history. It would be useful to evaluate the niches occupied by the various components of the flora and test whether invasives are found in different niches to natives. If true, this might not be entirely due to phylogenetic relationships, but our MPD results certainly suggest it plays a role. Schaefer and co-workers (2011) found that PNND explains invasiveness to a degree, but ecological characteristics, such as seed size and life form, are important in determining invasion success. We have not tested for the influence of ecological traits and these may contribute to the pattern observed. Nevertheless, they are unlikely to explain the pattern fully (Schaefer et al. (2011) demonstrated that it was only a component of invasive success), and many of these traits are likely to be phylogenetically conserved.

Some studies have also found mixed results with regard to Darwin's hypothesis. For example, Maitner et al. (2011) showed that an introduced community of invasive birds was assembled via habitat filtering (i.e. invasive species were often closely related to native species) rather than through exclusion due to competitive interactions as expected under Darwin's hypothesis. In contrast, the phylogenetic pattern we found is strong, unlikely to be driven by chance (Figure 2.13) and, given its support at the local scale, we argue that it is evidence in support of Darwin's naturalisation hypothesis acting at various scales in the success of plant invaders on Robben Island. Davies, Cavender-Bares & Deacon (2011) also assessed the use of phylogenetic metrics to predict invasion success of introduced grasses in a serpentine ecosystem of northern California. They found the same pattern, that is, successful invaders were less related to native, and that the native to invasive distance was much longer at smaller scales (see also Strauss, Webb & Salamin 2006; Proches et al. 2008). Schaefer et al. (2011) also revealed a pattern consistent with Darwin's expectations in the Azores flora, with the additional caveat that a combination of phylogenetic data and ecological features would enhance our predictive power to explain invasiveness. The applicability of Darwin's naturalisation hypothesis to invasion management may therefore be taxonomic and/or ecologically context-dependent. Levine, Adler & Yelenik (2004) suggested that biotic resistance of native species in a given community might cause the increased distance between natives and invasives. They surveyed the literature for studies regarding the role of biotic resistance in the successful establishment of invaders in new environments. This meta-analysis showed that most native systems limit invasion success of aliens as a result of strong competitive interactions between native and alien taxa. Weak competitors are likely to be eliminated from the community as a result of such interactions, supporting the idea that alien species, which have established on Robben Island, are sufficiently strong competitors.

Critically, our study adds to the body of literature that evolutionary metrics, such as PNND, can help predict potential invaders. South Africa is developing an 'early warning programme' for potential invasives and evolutionary metrics may be incorporated into the programme in addition to more traditional ecological assessments (Hayes & Barry 2008; Küster et al. 2008; Dawson, Burslem & Hulme 2009). Robben Island, just like New Zealand (Duncan & Williams 2002; Diez et al. 2009), Hawaii (Daehler 2001) or the Azores (Schaefer et al. 2011), has provided excellent case studies to showcase the non-randomness of invaders. With next generation DNA sequencing and global efforts in assembling the tree of life, we can expect studies like mine to expand at much larger scales. Particularly in South Africa where invasive species are a major issue (van Wilgen et al. 2001) and the native flora is well sampled from a phylogenetic perspective (Forest et al. 2007), it would be feasible to integrate evolutionary and ecological metrics to tackle some of the problems posed by alien species. Clearly, more work is needed before our research can be fully integrated in these conservation efforts.

CHAPTER THREE

ALIEN INVASIVE PLANTS ARE 'BACK-SEAT DRIVERS' OF LOSS IN PHYLOGENETIC DIEVRSITY IN NATIVE COMMUNITIES ON ROBBEN ISLAND

3.1. Introduction

Invasive alien species are well known for their contribution to ecological disruption, including alteration of ecosystem services and biodiversity loss (Holmes & Cowling 1997; Mack et al*.* 2000; Rice & Emery 2003; Clavero & García-Berthou 2005; Winter et al*.* 2009). Various systems (plants, vertebrates, invertebrates, etc.) have been documented, and showed huge invasion success especially on islands (Eldredge & Miller 1995; Chown et al*.* 1998; Sax et al*.* 2002; Sax & Gaines 2003; Blackburn et al*.* 2004). Their introduction and naturalisation may result in an increase of net species richness of the islands (Eldredge & Miller 1995; Sax & Gaines 2003; Blackburn et al*.* 2004; Sax & Gaines 2006). However, it could also result in dramatic consequences for native communities. For example, the avifauna of New Zealand has suffered a great loss of 38 of its 91 native land birds, and at least three native plants went extinct (Sax et al. 2002).

Although impacts of alien invasives on native bird diversity seem to be well established, very little is known about the loss of native plant species (Blackburn et al*.* 2004; Clavero & Garcia-Berthou 2005; Sax & Gaines 2008), especially the loss of evolutionary diversity. Such loss of evolutionary history will progressively lead to genetic homogenisation (Winter et al. 2009), which is of great concern from a conservation perspective (Forest et al. 2007; Gilbert & Webb 2007; Knapp et al. 2008; Sax & Gaines 2008).

The success of invasion management is dependent upon the model of invasion that operates in a particular area of concern (Bauer 2012). Different models have been suggested, all relying on the key drivers of ecosystem alteration. Invasives could be 'passengers', 'back-seating drivers' or 'drivers' of change in native community composition (MacDougall & Turkington 2005; Bauer 2012). In the 'passenger' model, invasives are not the cause of ecosystem disruption and diversity loss but rather a 'symptom' of this alteration, i.e. invasives are just bio-indicators of landscape disruption (Bauer 2012). In 'back-seating driver' model, invasives are also not the direct cause of biodiversity loss, which is actually caused by ecosystem disturbances. They are just beneficiary of these disturbances, which favour their invasion success (naturalisation) because they might be more tolerant to disturbances than native species. The naturalisation coupled with the invasion success will result in a further alteration of native communities. In contrast, under the 'driver model', invasives are the direct cause of biodiversity loss and ecosystem disruption.

When biological invasion occurs, management planning generally focuses on removal of invasives; but recent studies indicate that the success of invasion management is directly linked to the relative importance of the invasion model that best-fits the changes in question (Bauer 2012). When invasives are just passengers of ecosystem disruption, then only ecosystem restoration, but not removal of invasives, could lead to the recovery of native communities. If invasives are back-seat drivers of ecosystem change, an effective management plan should include both the removal of invasives and the control of primary drivers of the disruption. Under the driver model, removing invasives from the invaded area is expected to promote a quick and full recovery of the community (Bauer 2012).

Here, I quantified the loss of phylogenetic diversity in native plant communities compared to expectation, and investigated the possible drivers (human induced disturbances and alien invasive plants) of this loss.

3.2. Materials and methods

3.2.1. Community sampling

The analysis in this Chapter focuses on 127 communities (plots as indicated in Chapter 2), and an additional two communities referred to as ‘Native’ and ‘Invasive’ communities. Native community is a community I generated with all native species found in the 127 plots; and invasive community includes all alien invasive species recorded in the 127 plots. In total 129 plots were analysed.

3.2.2. Data analysis

I quantified the species richness ($SR_{observed}$) and phylogenetic diversity ($PD_{observed}$) of all 129 communities. Then, using the null model ‘richness’ and the function ‘ses.pd’ implemented in the R package PICANTE 1.2. (Kembel et al. 2010), I quantified the PD expected ($PD_{expected}$) under the scenario that communities are just a random collection of species on the Island. $PD_{expected}$ is the PD of communities assembled by neutral forces, i.e. their composition is not dictated by any constrains whatsoever (e.g. ecological constrains). Therefore, the comparison of $PD_{observed}$ vs. $PD_{expected}$ is expected to reveal the effects of constrains, if any, on the amount of evolutionary information (PD) accumulated in each community. For example, if for a community $PD_{observed} < PD_{expected}$, it would indicate that there are some ecological forces that limit the amount of PD of that community; if $PD_{observed} > PD_{expected}$, the ecological forces may be favouring accumulation of PD; but $PD_{observed} = PD_{expected}$ is indicative of community composition dictated by neutral forces.

To further assess the phylogenetic structure of communities, I calculated the net relatedness index (NRI) of all communities. NRI was calculated using the ‘ses.mpd’ function in PICANTE 1.2. Positive values of NRI indicate that closely related species co-occur more often than predicted by chance (phylogenetic clustering), whereas negative values indicate greater co-occurrence of more distantly related species (phylogenetic overdispersion). I assessed significance of NRI using 1,000 simulations and using the phylogeny reconstructed (Chapter 2) as the regional pool (null model “phylogeny.pool” in PICANTE 1.2).

In addition to the 129 plots indicated above, I created another community called ‘Robben’ where all species (native and alien) are included, thus 130 communities in total. I then measured patterns of phylogenetic relatedness among all communities (phylogenetic beta diversity), i.e. the mean phylogenetic distance between pairs of communities (MPD_{com}). This is performed using the function ‘comdist’ in the R package PICANTE 1.2. Values of MPD_{com} were then used in a cluster analysis or phylo-ordination to group communities based on their evolutionary similarity.

3.3. Results

3.3.1. Diversity on the Island

Plant diversity was measured as SR and PD. Species richness varies from 6 to 19 species per community, with an average of 12.16 species, but the evolutionary history accumulated ($PD_{observed}$) was estimated to 610.1512-1243.57 million years, with an average of 902.3429 Myrs (Table 1). Further to this, there was almost a perfect 1 to 1 match between the number of invasive alien and native plant species in all the 127 plots ($SR_{Invasive} = SR_{Native} = 25$ species). However, invasive community had a PD higher than that of native ($PD_{Invasive} = 1496.271$ Myrs vs. $PD_{Native} = 1043.655$ million years; Table 3.1).

3.3.2. Community structure on the Island

The vast majority of NRI values for the 127 plots were negative (Table 3.1), indicating that communities were more overdispersed than expected by chance. However, looking specifically at community structure of invasive and native communities, I found $NRI_{Invasive} > 0$ ($NRI_{Invasive} = 0.89$) and $NRI_{Native} > 0$ ($NRI_{Native} = 1.80$), suggesting that invasives and natives were not just a random collection of species on the island, i.e. they were more closely related than expected by chance. However, assessing relatedness of invasives vs. natives, I found $NRI_{Invasive} < NRI_{Native}$, indicating that invasives were more overdispersed than natives.

3.3.3. Phylogenetic beta diversity on the island

In an attempt to assess how related communities are on the island (unlike how related species are within communities), I computed the phylo-ordination of all 130 communities with the objective of observing specifically the grouping of Native vs. Invasive vs. Robben communities (Figure 3.1). Invasive community (indicated with a red dot) groups with Robben (blue dot) whereas Native groups alone (green dot) on this phylo-ordination.

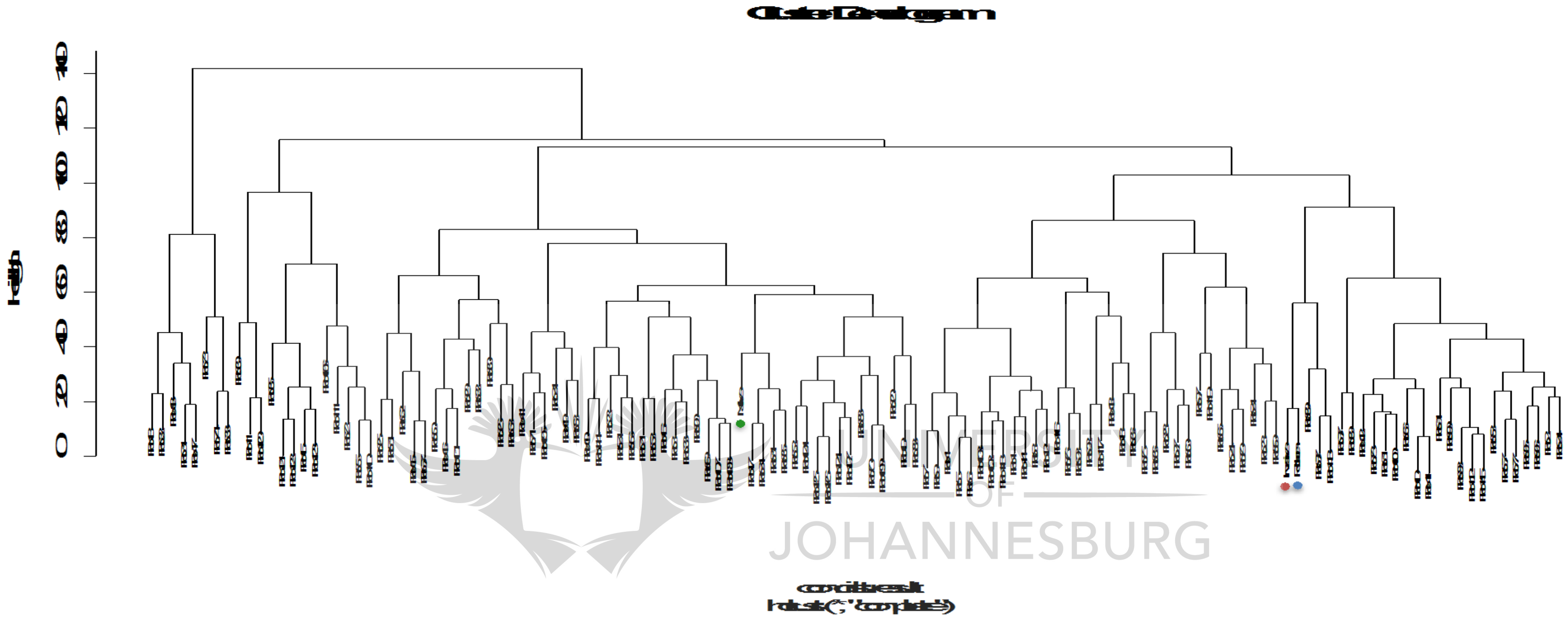


Figure 3.1. Phylo-ordination of plant communities on Robben Island. Communities are grouped based on their mean pairwise distance (MPD_{com}; see text for details). Green dot indicate the position of native community; red dot indicates the position of invasive community; and blue dot indicates the position of Robben community as defined in this study (see text for details.

Table 3.1. Pattern of diversity and community metrics on Robben Island. PD = phylogenetic diversity; SR = species richness; NRI = net relatedness index; p indicates significance of NRI metrics; Sample labeled ‘Invasive’ include all invasive species recorded in all 127 plots; and sample labeled ‘Native’ include all native species recorded in all 127 plots.

Samples	PD	SR	NRI	p
Plot1	1061.649	14	-0.57432	0.687
Plot2	1199.162	17	-0.95384	0.843
Plot3	991.517	14	-0.77952	0.776
Plot4	1236.423	16	-1.14473	0.903
Plot5	1228.303	15	-1.40816	0.973
Plot6	1230.445	16	-1.57288	0.988
Plot7	1168.585	15	-1.19199	0.925
Plot8	1106.356	16	-1.45109	0.967
Plot9	1159.668	14	-1.73339	0.996
Plot10	705.7871	9	-0.93675	0.842
Plot11	740.9894	10	-0.54038	0.667
Plot12	1053.345	13	-1.53414	0.984
Plot13	934.5776	12	-1.16949	0.917
Plot14	1243.57	16	-1.74848	0.997
Plot15	1051.623	14	-1.091	0.905
Plot16	1048.657	15	-1.0745	0.885
Plot17	639.1668	7	-0.88146	0.815
Plot18	709.7539	8	-0.61904	0.694
Plot19	760.1606	10	-0.6381	0.709
Plot20	865.6316	11	-1.00849	0.879
Plot21	841.3776	13	0.183765	0.340
Plot22	610.1512	8	-0.4426	0.611
Plot23	1091.17	15	-0.98031	0.838
Plot24	836.5406	10	-1.35447	0.956
Plot25	819.0979	11	-0.62585	0.700
Plot26	628.7274	7	-0.57773	0.691
Plot27	858.4225	12	-0.67183	0.736
Plot28	975.6567	15	-1.17931	0.921
Plot29	972.6052	12	-1.03925	0.888
Plot30	837.653	11	-0.46594	0.620
Plot31	1054.417	14	0.954899	0.154
Plot32	715.0699	10	1.161882	0.122
Plot33	952.567	13	-1.02248	0.877
Plot34	808.6421	9	-1.32906	0.972
Plot35	726.4671	8	-1.29466	0.970
Plot36	817.6638	11	-0.80788	0.797
Plot37	640.9863	9	-0.25075	0.523
Plot38	831.5599	10	-1.21678	0.942
Plot39	875.2167	11	-0.03392	0.415

Samples	PD	SR	NRI	p
Plot40	826.048	12	-0.73868	0.761
Plot41	761.3781	10	-1.03409	0.895
Plot42	992.8511	13	-1.23663	0.937
Plot43	1108.642	14	-0.67833	0.741
Plot44	1103.331	15	0.243425	0.345
Plot45	828.8871	12	-0.00638	0.426
Plot46	891.3179	12	-1.10708	0.907
Plot47	1007.503	12	-0.45323	0.609
Plot48	933.7884	12	0.576368	0.243
Plot49	1096.597	13	-1.18157	0.929
Plot50	752.8843	11	-0.28462	0.551
Plot51	742.6664	9	-0.51492	0.628
Plot52	967.5867	12	-1.11772	0.897
Plot53	910.2284	10	-1.43317	0.987
Plot54	664.0863	9	-0.35694	0.571
Plot55	836.5253	11	-0.03333	0.448
Plot56	669.6532	10	1.068114	0.149
Plot57	886.9652	12	-1.36289	0.951
Plot58	1066.36	14	-1.2953	0.944
Plot59	915.2194	11	-1.69444	0.997
Plot60	657.3517	7	-1.35677	0.987
Plot61	899.5992	12	-0.91913	0.845
Plot62	891.248	13	1.360443	0.102
Plot63	655.2412	8	-0.17479	0.487
Plot64	768.4942	11	-0.06067	0.445
Plot65	884.3876	11	-0.89543	0.811
Plot66	918.7704	13	-0.34444	0.570
Plot67	874.3911	11	-0.37676	0.586
Plot68	921.9287	11	-0.37942	0.575
Plot69	973.9464	15	0.100061	0.392
Plot70	1038.259	16	-0.75919	0.766
Plot71	1200.941	16	-0.6273	0.711
Plot72	1006.999	15	-0.654	0.731
Plot73	652.2219	8	1.060746	0.154
Plot74	783.7872	13	2.59006	0.021
Plot75	858.9336	11	-1.32197	0.964
Plot76	874.8599	11	-1.01589	0.855
Plot77	877.3025	11	-1.34363	0.976
Plot78	860.8749	12	-0.61317	0.704
Plot79	708.725	8	-1.24799	0.942
Plot80	797.0586	10	-0.28827	0.525
Plot81	820.4445	11	-0.34149	0.550
Plot82	865.4881	11	-0.69806	0.743
Plot83	785.8578	12	2.399939	0.029
Plot84	745.4864	9	-1.27439	0.948
Plot85	851.6133	11	0.01812	0.398
Plot86	759.3406	8	-1.53743	0.990
Plot87	919.6487	13	-0.27227	0.541
Plot88	984.7206	13	-1.23363	0.934

Samples	PD	SR	NRI	p
Plot89	1016.651	15	-0.74714	0.765
Plot90	704.677	10	-0.32196	0.543
Plot91	1012.534	14	-0.69388	0.736
Plot92	820.5833	11	-0.97011	0.865
Plot93	1032.622	14	-1.4116	0.969
Plot94	1176.707	17	-0.92718	0.832
Plot95	930.3076	12	-0.3339	0.579
Plot96	856.2336	11	-1.12475	0.910
Plot97	660.7252	9	-0.39793	0.585
Plot98	694.124	9	-0.31794	0.545
Plot99	917.5541	14	0.376524	0.287
Plot100	996.4613	14	-0.52545	0.645
Plot101	998.3919	15	-0.91002	0.829
Plot102	973.8782	13	-1.12992	0.919
Plot103	1236.266	17	-0.95321	0.852
Plot104	1052.118	16	0.166011	0.372
Plot105	1247.983	17	-0.90869	0.825
Plot106	884.6227	11	-0.23951	0.520
Plot107	985.528	14	-0.60415	0.708
Plot108	819.9856	12	-0.31803	0.566
Plot109	1066.959	16	-0.9984	0.860
Plot110	976.2467	14	-0.94925	0.835
Plot111	789.7619	12	-0.13523	0.486
Plot112	822.8133	13	0.409951	0.293
Plot113	979.9679	14	-0.86961	0.815
Plot114	638.2924	10	0.089651	0.408
Plot115	765.9429	11	-0.31984	0.553
Plot116	770.1663	9	-0.46609	0.630
Plot117	611.0428	6	-1.18714	0.944
Plot118	1005.309	14	-1.1671	0.918
Plot119	913.7961	14	-0.92667	0.831
Plot120	818.6988	11	-1.00957	0.880
Plot121	1028.056	14	-1.21331	0.949
Plot122	1217.267	19	-1.13	0.906
Plot123	895.524	12	-1.11613	0.892
Plot124	932.2085	14	-0.73761	0.744
Plot125	931.1996	15	-0.28765	0.547
Plot126	826.0146	12	-0.81801	0.795
Plot127	964.8592	13	-1.06443	0.894
Invasive	1496.271	25	0.888809	0.195
Native	1043.655	25	1.798228	0.059

3.3.4. Comparison of PD observed versus PD expected

Considering only invasives vs. natives at island scale, I found that for community of natives, $PD_{observed}$ was significantly lower than $PD_{expected}$ (1045.24 vs. 1402.08 million years; $p = 0.001$; Table 3.2), indicating that natives are underdispersed. Considering all invasive alien species together, I found that $PD_{observed}$ was slightly but not significantly higher than $PD_{expected}$ (1497.856 vs. 1392.158 Myrs; $p > 0.05$), indicative of a trend towards phylogenetic overdispersion of alien communities. It also clearly appears that $PD_{observed}$ for natives (PD = 1045.24 Myrs) is lower than that of invasives (PD = 1497.86 Myrs).

At a smaller scale where invasives and natives co-occur (i.e. in the 127 plots), I found that $PD_{observed}$ was generally higher than expected (Table 3.2), consistent with the overdispersion pattern revealed by NRI analysis.

Table 3.2. Comparison of observed PD vs. expected; ntaxa = Number of taxa in samples; pd.obs = Observed PD; pd.rand.mean = Mean PD in null communities; pd.rand.sd = Standard deviation of PD in null communities; pd.obs.rank = Rank of observed PD vs. null communities; pd.obs.z = Standardised effect size of PD vs. null communities (= (pd.obs - pd.rand.mean) / pd.rand.sd); pd.obs.p = p-value (quantile) of observed PD vs. null communities (= mpd.obs.rank / runs + 1); runs = Number of randomisations

Samples	ntaxa	pd.obs	pd.rand.mean	pd.rand.sd	pd.obs.rank	pd.obs.z	pd.obs.p	runs
Invasive	25	1497.856	1392.157809	90.6182	880	1.166408	0.88	999
Native	25	1045.24	1402.076987	91.94065	1	-3.88117	0.001	999
Plot1	14	1063.233	958.7982237	78.91423	901	1.323402	0.901	999
Plot2	17	1200.747	1091.364871	84.89642	903	1.288419	0.903	999
Plot3	14	993.1017	957.3709451	82.69016	643	0.432104	0.643	999
Plot4	16	1238.008	1046.891482	85.19477	990	2.24329	0.99	999
Plot5	15	1229.888	1004.000987	83.86852	1000	2.693348	1	999
Plot6	16	1232.03	1039.820925	87.02053	988	2.208774	0.988	999
Plot7	15	1170.17	1007.079952	84.00356	976	1.941461	0.976	999
Plot8	16	1107.94	1053.100727	84.6029	736	0.648201	0.736	999
Plot9	14	1161.252	957.4117877	81.88275	995	2.48942	0.995	999
Plot10	9	707.3718	708.8406034	69.23129	458	-0.02122	0.458	999
Plot11	10	742.5741	768.4267216	70.2962	361	-0.36777	0.361	999
Plot12	13	1054.93	914.879203	81.29956	967	1.722651	0.967	999
Plot13	12	936.1623	862.5572317	73.96957	839	0.995073	0.839	999
Plot14	16	1245.155	1043.90117	85.97909	994	2.340725	0.994	999
Plot15	14	1053.208	961.1680281	85.41811	857	1.077524	0.857	999
Plot16	15	1050.241	1000.784204	82.37726	715	0.600373	0.715	999
Plot17	7	640.7515	592.5634392	63.21892	764	0.762241	0.764	999
Plot18	8	711.3386	651.6771	70.1352	799	0.850664	0.799	999
Plot19	10	761.7453	765.7651705	75.37369	454	-0.05333	0.454	999

Samples	ntaxa	pd.obs	pd.rand.mean	pd.rand.sd	pd.obs.rank	pd.obs.z	pd.obs.p	runs
Plot20	11	867.2163	817.9949872	75.97271	724	0.647881	0.724	999
Plot21	13	842.9623	918.2081974	81.43377	170	-0.92401	0.17	999
Plot22	8	611.7359	647.412176	71.32427	287	-0.5002	0.287	999
Plot23	15	1092.755	1004.828419	86.82038	842	1.01274	0.842	999
Plot24	10	838.1253	764.1114525	74.35245	839	0.995445	0.839	999
Plot25	11	820.6826	813.001766	76.91008	524	0.099867	0.524	999
Plot26	7	630.3121	594.5447938	65.26226	697	0.548055	0.697	999
Plot27	12	860.0072	865.4463043	76.51065	442	-0.07109	0.442	999
Plot28	15	977.2414	1004.858882	82.86314	367	-0.33329	0.367	999
Plot29	12	974.1899	862.165717	81.68808	916	1.371365	0.916	999
Plot30	11	839.2377	813.7319472	75.96297	624	0.335766	0.624	999
Plot31	14	1056.002	960.8178687	82.48219	886	1.153997	0.886	999
Plot32	10	716.6546	766.0036887	74.50848	244	-0.66233	0.244	999
Plot33	13	954.1517	911.3407189	78.45122	696	0.545702	0.696	999
Plot34	9	810.2268	710.7831457	72.46088	922	1.372377	0.922	999
Plot35	8	728.0518	651.6010534	69.00582	872	1.107888	0.872	999
Plot36	11	819.2485	815.5069275	75.34253	514	0.04966	0.514	999
Plot37	9	642.571	715.8633313	67.62609	130	-1.08379	0.13	999
Plot38	10	833.1446	762.8285775	77.12819	812	0.911677	0.812	999
Plot39	11	876.8014	815.7117169	75.36766	789	0.810556	0.789	999
Plot40	12	827.6327	864.9120328	80.27087	307	-0.46442	0.307	999
Plot41	10	762.9628	762.0928858	73.31251	481	0.011866	0.481	999
Plot42	13	994.4358	919.0456993	78.68938	835	0.958073	0.835	999
Plot43	14	1110.227	961.3128858	81.03282	971	1.837698	0.971	999
Plot44	15	1104.916	1007.335963	84.26329	873	1.158035	0.873	999
Plot45	12	830.4718	861.9313245	77.56714	335	-0.40558	0.335	999
Plot46	12	892.9026	863.1168959	79.26933	628	0.375754	0.628	999
Plot47	12	1009.088	867.6677871	78.19508	969	1.808555	0.969	999
Plot48	12	935.3731	863.4716201	77.5443	828	0.927231	0.828	999

Samples	ntaxa	pd.obs	pd.rand.mean	pd.rand.sd	pd.obs.rank	pd.obs.z	pd.obs.p	runs
Plot49	13	1098.182	914.0465119	80.0276	991	2.300894	0.991	999
Plot50	11	754.469	811.2555744	76.16353	233	-0.74559	0.233	999
Plot51	9	744.2511	712.0137723	70.10123	664	0.459868	0.664	999
Plot52	12	969.1714	863.1252847	75.48375	935	1.404887	0.935	999
Plot53	10	911.8131	761.9478729	73.22567	990	2.046622	0.99	999
Plot54	9	665.671	709.3901502	69.26351	247	-0.6312	0.247	999
Plot55	11	838.11	819.7601235	73.68347	575	0.249036	0.575	999
Plot56	10	671.2379	768.848073	76.17557	106	-1.28138	0.106	999
Plot57	12	888.5499	867.5794666	76.08804	602	0.275608	0.602	999
Plot58	14	1067.945	958.1312836	81.44499	909	1.348316	0.909	999
Plot59	11	916.8041	816.3222549	77.36828	919	1.298747	0.919	999
Plot60	7	658.9364	591.769607	62.41098	859	1.076201	0.859	999
Plot61	12	901.1839	866.443415	77.42485	650	0.448699	0.65	999
Plot62	13	892.8327	912.5394069	79.15139	383	-0.24898	0.383	999
Plot63	8	656.8259	655.2978446	67.20921	472	0.022735	0.472	999
Plot64	11	770.0789	817.1115984	75.2919	262	-0.62467	0.262	999
Plot65	11	885.9723	813.7842754	73.84327	841	0.977584	0.841	999
Plot66	13	920.3551	916.6231112	82.72163	510	0.045116	0.51	999
Plot67	11	875.9758	814.759015	76.12764	784	0.804134	0.784	999
Plot68	11	923.5134	813.6682533	79.98906	928	1.373252	0.928	999
Plot69	15	975.5311	1005.109339	83.87115	361	-0.35266	0.361	999
Plot70	16	1039.844	1048.583541	89.70353	458	-0.09743	0.458	999
Plot71	16	1202.526	1044.239374	82.5125	981	1.918332	0.981	999
Plot72	15	1008.584	1006.403466	84.30921	506	0.025861	0.506	999
Plot73	8	653.8066	652.2802971	69.03884	463	0.022107	0.463	999
Plot74	13	785.3719	914.9311884	78.78277	56	-1.64451	0.056	999
Plot75	11	860.5183	819.6230422	76.00278	688	0.538076	0.688	999
Plot76	11	876.4446	815.2831667	77.65974	789	0.787556	0.789	999
Plot77	11	878.8872	818.1665366	70.90111	801	0.856413	0.801	999

Samples	**ntaxa**	**pd.obs**	**pd.rand.mean**	**pd.rand.sd**	**pd.obs.rank**	**pd.obs.z**	**pd.obs.p**	**runs**
Plot78	12	862.4596	865.9853967	77.52061	487	-0.04548	0.487	999
Plot79	8	710.3097	651.7121394	67.97867	799	0.861999	0.799	999
Plot80	10	798.6433	761.5041897	77.06916	669	0.481894	0.669	999
Plot81	11	822.0292	812.098845	75.51619	515	0.1315	0.515	999
Plot82	11	867.0728	817.1054361	77.51783	720	0.644591	0.72	999
Plot83	12	787.4425	866.6111722	81.27905	171	-0.97404	0.171	999
Plot84	9	747.0711	707.1940231	71.48654	700	0.557826	0.7	999
Plot85	11	853.198	820.2000574	74.39838	658	0.443531	0.658	999
Plot86	8	760.9253	656.1346157	66.23023	960	1.582218	0.96	999
Plot87	13	921.2334	916.0888179	80.75194	522	0.063708	0.522	999
Plot88	13	986.3053	916.3829865	81.74296	809	0.855392	0.809	999
Plot89	15	1018.236	1006.946807	82.46762	530	0.136888	0.53	999
Plot90	10	706.2617	764.5718735	77.11078	211	-0.75619	0.211	999
Plot91	14	1014.119	958.3858977	80.54419	754	0.691957	0.754	999
Plot92	11	822.168	818.8586798	73.73736	503	0.04488	0.503	999
Plot93	14	1034.207	963.7886517	79.80358	819	0.882391	0.819	999
Plot94	17	1178.291	1094.233974	85.22431	835	0.986308	0.835	999
Plot95	12	931.8923	869.1650426	79.28467	776	0.791165	0.776	999
Plot96	11	857.8183	818.404935	75.28508	690	0.523522	0.69	999
Plot97	9	662.3099	708.5393796	70.18637	232	-0.65867	0.232	999
Plot98	9	695.7087	709.0717029	69.17493	398	-0.19318	0.398	999
Plot99	14	919.1388	959.2435555	81.50599	303	-0.49205	0.303	999
Plot100	14	998.046	959.307374	83.51774	678	0.463837	0.678	999
Plot101	15	999.9766	1004.910063	81.0928	464	-0.06084	0.464	999
Plot102	13	975.4629	911.8309666	85.54845	765	0.743812	0.765	999
Plot103	17	1237.85	1092.638795	90.27566	947	1.608535	0.947	999
Plot104	16	1053.703	1047.976465	84.58954	507	0.067695	0.507	999
Plot105	17	1249.567	1089.804133	87.39014	977	1.828161	0.977	999
Plot106	11	886.2074	812.1259228	75.55582	833	0.980487	0.833	999

Samples	ntaxa	pd.obs	pd.rand.mean	pd.rand.sd	pd.obs.rank	pd.obs.z	pd.obs.p	runs
Plot107	14	987.1127	958.6263656	81.38008	626	0.350041	0.626	999
Plot108	12	821.5703	862.3359969	75.17784	269	-0.54226	0.269	999
Plot109	16	1068.543	1049.480527	82.78704	579	0.230264	0.579	999
Plot110	14	977.8314	961.0866465	82.35255	572	0.20333	0.572	999
Plot111	12	791.3466	868.1782985	78.96419	170	-0.97299	0.17	999
Plot112	13	824.398	912.2899071	79.57762	135	-1.10448	0.135	999
Plot113	14	981.5526	959.7027835	79.11097	608	0.276192	0.608	999
Plot114	10	639.8771	765.1258065	74.17316	53	-1.6886	0.053	999
Plot115	11	767.5276	820.3444355	75.584	234	-0.69878	0.234	999
Plot116	9	771.751	713.1560092	68.91608	809	0.850237	0.809	999
Plot117	6	612.6275	531.7415724	62.55194	930	1.293101	0.93	999
Plot118	14	1006.893	957.3506883	84.94519	715	0.583231	0.715	999
Plot119	14	915.3808	958.708858	79.93327	289	-0.54205	0.289	999
Plot120	11	820.2835	816.2420239	76.30655	504	0.052963	0.504	999
Plot121	14	1029.64	961.783953	80.47221	796	0.843227	0.796	999
Plot122	19	1218.851	1169.791081	87.6386	716	0.559801	0.716	999
Plot123	12	897.1087	865.7048453	76.88106	641	0.408473	0.641	999
Plot124	14	933.7932	959.338159	82.53507	368	-0.3095	0.368	999
Plot125	15	932.7843	1002.244236	80.94602	197	-0.8581	0.197	999
Plot126	12	827.5993	864.83568	77.71844	316	-0.47912	0.316	999
Plot127	13	966.4439	916.9681446	80.00021	718	0.618445	0.718	999

3.4. Discussion

Looking at dispersion of natives vs. invasives at the island scale, I found that native species on the island show lower PD than invasive alien species. In addition, I found that they also accumulated lower PD (i.e. are more clustered) than expected by chance. These findings are indicative of underlying forces that are limiting native phylogenetic diversity. If these forces keep operating, this might lead to the homogenisation of native community on the island (see also Winter et al. 2009). Habitat filtering might be the cause of the observed pattern (Webb et al. 2002; but see Mayfield & Levine 2010 for role of competition). Recent studies indicated that disturbances operate as key environmental filters that limit species co-existence, therefore leading to clustered communities (Helmus et al. 2010).

Over the past four centuries, vegetation of the Island has been severely disturbed by human activities (see Chapter 1 for details). In addition, overgrazing by livestock (e.g. deer's) may also be detrimental to the natural vegetation on Robben Island (Boucher 1983). As a result of these disturbances, native vegetation (evergreen shrubs, perennial grasses and annual geophytes) similar to that of the West Coast Strandveld (Adamson 1934) has disappeared. Given the degree of disturbances on the island, I argue that the lower PD observed for native community is more likely a result of centuries of human-induced disturbances.

However, the question here is what is the role of alien species in lowering PD of native communities? I therefore looked at plant dispersion at smaller scale (i.e. at plot levels) where alien invasive and native co-occur. I found that communities are overdispersed. Alien species might be more tolerant to disturbances than natives (Didham et al. 2005; MacDougall & Turkington 2005). As such, disturbances could weaken resistance and competitive ability of natives (Levine et al. 2004), which therefore will progressively disappear from the ecosystems in the face of invasive aggression, allowing alien species to dominate. This is likely the case here, because the post-disturbance events have been marked by at least 42% of the island being covered by alien vegetation (Chapman et al. 2000). Such huge invasive success is reflected in the evolutionary information accumulated by the flora of Robben Island being more closely similar to that of invasive than to natives (see phylo-ordination in Figure 3.1). If disturbances and plant introduction continue, alien expansion is expected to increase (see Sax et al. 2002; Clavero & García-Berthou 2005; Winter et al. 2009). Therefore, human-induced disturbances but not invasive alien species are the direct drivers of landscape change on the island. Since invasives might be favoured by disturbances, they dominate the island, further reducing native diversity. As such, invasives are 'back-seat drivers' (Bauer 2012) of diversity loss in native community.

The disappearance of natives (more likely due to low competitive ability to survive in disturbed environment) might result in more opened niches that could be filled by naturalised alien species (more resistant to disturbances). In such scenario where both natives and alien compete for their persistence in the ecosystems, if this competitive ability is conserved (which is more likely, see Wiens et al. 2010), coexistence of natives and invasives will lead to community overdispersion (Webb et al. 2002; Cavender-Bares et al. 2004). This is exactly the pattern I observed.

There is a general concern that invasives disrupt ecosystem sustainability (Sax et al. 2002; Clavero & Garcıa-Berthou 2005; Winter et al. 2009). As invasion rate is expected to increase on islands (Sax et al*.* 2002; Steadman 2006; Sax & Gaines 2008), the effects of invasives could be even more destructive on native communities (Winter et al*.* 2009), if adequate management decision is not taken.

Importantly, I found that the back-seat driver model is more suitable to explain the role of invasives in reducing the PD of native community. This has implication for invasion management on the island. Following Bauer (2012), an effective management plan of alien invasive should include not only the removal of invasives, but also the control of primary driver of invasion success on the island which is clearly ecosystem disturbances.

Conservation officers have recently decided to re-introduce native plants on the island. The current physiognomy of the island indicates that it is a disturbed environment (Figures 2.2A & 2.2B in Chapter 2). Thus the re-introduction of native species may therefore cause some of these species to become even more invasive in such disturbed area where their natural enemies, that can regulate their establishment, might already be removed. Therefore, I suggest a progressive removal of alien invasives, the limitation of causes of disturbances without any re-introduction, with the expectation that native community will recover on its own over time.

3.5. Conclusion

There is an increasing concern about the impacts of invasive alien species on South African rich biodiversity. I investigate the impacts of invasives on native community on Robben Island. I found that phylogenetic diversity of native species has declined compared to the expectation. I argue that disturbances may promote invasion of alien plants (42% of the island have been invaded after disturbances occurred), which in turn has significantly reduced the phylogenetic diversity of native species, certainly due to their higher competitive ability. This study contributes to the ongoing debate over the role invasive plants play in causing declines in biodiversity worldwide.

CHAPTER 4

GENERAL CONCLUSION

Currently, there is an ongoing debate, pioneered by the Robben Island Museum (RIM) about the implementation of a management plan that can lead to the recovery of the natural vegetation. At the core of this debate lies the removal of alien invasive species from the island. In an attempt to fuel this debate, I do believe that three major questions should be addressed.

First, are invasive species the major drivers of loss in native community composition on Robben Island? Previous studies showed that prior to human settlement, the physiognomy of the flora of the island was similar to the current West Coast Strandveld, and that the post-period of human interference has resulted not only in a decline of native diversity, but also in a rapid spread of alien species, leading to over 42% of the island being invaded (Chapman et al*.* 2000). Such observations clearly indicate that human-induced disturbances are the major drivers of ecosystem disturbances on the island, and these disturbances may favour invasion of aliens over natives.

Second, is relatedness among species playing an important role in invasive success of aliens on Robben Island? In the current study, I use a phylogenetic approach to address this question. Following Darwin (1859), closely related species are expected to co-occur less often, given their shared affinities for similar environmental conditions. As such, introduced plant species are therefore expected to eventually establish a self-sustaining population in their new environment only if they are phylogenetically less related to the native community (Darwin's naturalisation hypothesis). I tested this hypothesis on Robben Island, and the results showed strong support to this expectation. I found that invasive alien plants are indeed more distantly related to the native flora, than any pair of native or invasive species (Chapter 2). Based on these finding, I argue that ecosystem alteration might be more stressful to natives than aliens, causing aliens (probably pre-adapted to disturbed environment) to outcompete natives and take over the island.

Third, since disturbances on the island have been considerably reduced over the past 20 years, what is the current impact of invasives on native plants on Robben Island? The native community on the island has not been recovered so far, and this is very concerning for local conservation authorities. The disturbances have caused severe species loss in native community, thus opening new niches (maybe previously occupied by natives) that facilitate the invasion by aliens. The communities over dispersion pattern observed at plot level; suggest that competition might be the major driver of current species composition at small scale. The invasion success of aliens indicates that they might be higher competitors, contributing to further exclusion of natives (low competitor). If adequate management decision is not taken, there is a high risk of the island being phylogenetically homogenised, with closely related alien species dictating the future composition of the island's flora. To prevent such pattern, I propose the following recommendations:

1. As pointed out human-induced disturbances have been the major cause of ecosystem alteration and must be strictly limited on the island. This should include avoiding further introduction of alien species (animal and plants),

especially by tourists and the present inhabitants on the island who must be eco-friendly. A strict control at point of entry (i.e. harbour) should be enforced to prevent the addition of plant materials to the island especially as garden plants. This is a serious problem not just on the island but also in South Africa in general, which faces one of the biggest problems with invasive plants in the world. Therefore, one needs to be particularly vigilant with escape from gardens or introduced taxa that are distantly related to the South African flora.

2. Existing alien species must progressively be removed from the island. This will reduce alien-native competitive interactions. Both limitation in disturbances and the removal of alien are expected to favour native species to progressively recover and recolonise the island.

3. A complex of native species from the West Coast Strandveld may be rehabilitated on the island as they might induce a quick recovery of the native flora. This is because the West Coast Strandveld is presumably the island's original vegetation. However, one must be very cautious in this regard. The island is no longer at its original state i.e. at its pre-settlement environmental conditions. Therefore, a mass re-introduction of 'native' plant from West Coast Strandveld may cause these species to become even more invasive than expected. Such reintroduction must be tested in a limited area for several years, to investigate their behaviour and impact on current condition of the island.

4. Finally, examining the regions of high species diversity from the species richness index, I recommend that a fenced 50 x 50 m plot be laid out on a relatively undisturbed area on the island with all alien species cleared from this area. This preventative measure will act as a barrier to inhibit the entry of animals. Such a survey will be useful to determine what species will regenerate from the seed bank left in the soil and provide insights on what plant species can be re-introduced to the island.

CHAPTER 5

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