An assessment of *Melaleuca* (Myrtaceae) as invasive species in South Africa

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Declaration

By submitting this thesis/dissertation electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Date: March 2017

Chapters 2, 3, and 4 have been published (chapter 4 is in press). Chapter 5 is presented in the style of a journal manuscript. Work on Chapter 2 was started as part of a BSc Hons project in 2012, but this was expanded and improved on as part of my MSc. More details on contributions to the thesis are provided at the start of each specific chapter. Figures and tables are inserted in the text near first referencing and are therefore not listed in the Table of Contents. This thesis contains a single bibliography to minimise duplication of referencing across the chapters.

Thesis outline

Evaluating potentially invasive plants is an important part of invasive species management. Reports of several naturalized and invasive *Melaleuca* species in South Africa prompted an investigation into which species are in the country and of these which pose a risk. I evaluated two *Melaleuca* species in South Africa, differing in initial invasive risk profile (Chapters 2 and 3); assess the invasion status of *Melaleuca* species introduced to South Africa, while identifying errors in taxonomic identification (Chapter 4); and explored how some traits influence invasiveness in this group (Chapter 5).

In Chapter 2 I document and assess management options for the first reported invasion of *Melaleuca parvistaminea* Byrnes (initially identified as *M. ericifolia*) in the world, in the context of a South African wetland ecosystem. Delimitation surveys indicate that the entire invasion is restricted to three sites between Tulbagh and Wolseley in the Western Cape province and that populations are confined to areas that were currently or previously covered by pine plantations (primarily *Pinus radiata*). To estimate levels of abundance I surveyed 42 % of the three identified areas and found ~26 000 plants over 1800 ha (condensed canopy area of 1.15 ha). At least 63 % of recorded plants were seedlings or juveniles, mostly < 4yrs old, and most occurred in seasonally inundated (but not waterlogged) habitats. *Melaleuca parvistaminea* creates monospecific stands that overtop the native shrubland vegetation (Breede Shale Renosterveld) and is thus considered a potential transformer species. Species distribution modelling identified large areas of climatically suitable habitat in the Western Cape, pointing to substantial invasion debt for the species in South Africa. Felling triggers seed release from serotinous capsules, resulting in prolific seedling recruitment after winter rains (up to ~18 000 seedlings/m^2). No evidence of a soil-stored seed bank was found, and when plants are cut at ground level or treated with herbicide after cutting, plants do not resprout. The invasive populations of this water-dispersed species are close to major rivers (the Berg and Breede), but the intervening countryside is largely transformed and is unfavourable for establishment. Much of the area downstream from the invaded area is open vegetation that is unsuitable for major recruitment; this area would be easy to survey and detect small plants. Consequently, although the extent of invasion is large (potentially 9185 ha), the invasion can be delimited with some confidence, and eradication is considered achievable since seeds only survive for about a year, seedlings achieve maturity after 4 years, and the species is an obligate reseeder. Given the threats posed, eradication is desirable and *M. parvistaminea* should be listed as a category-1a invader (requiring compulsory control) under the Alien and Invasive Species Regulations of South Africa's National Environmental Management: Biodiversity Act (10/2004). I estimate that search-and-destroy operations could eradicate the species by 2021 at a cost of ZAR 3 475 000 (US$ 355400).

Chapter 3. The discovery of a naturalised population of *Melaleuca quinquenervia* in South Africa in 2009 prompted an evaluation of the species' distribution across South Africa. I found records at seven localities in two of the nine provinces of South Africa, with naturalized populations at two sites—~300 plants were discovered over 0.3ha in a confined-seep on a mountain slope, while at an old arboretum 12 large, planted trees and 9 naturalised trees were found. An additional herbarium record from Mozambique suggests that this global invader is present at other sites within the sub-region. This means that although the extirpation of populations in South Africa is recommended (and seems feasible), further work is required to determine the status and evaluate whether eradication from the sub-region is possible.

Chapter 4. Lists of introduced species provide essential background information to inform management of, and research on, biological invasions. The compilation of these lists is, however, prone to a variety of errors. I highlight the frequency and consequences of such errors using introduced *Melaleuca* (sensu lato, including *Callistemon*) species in South Africa as a case study. I examined 111 herbarium specimens from South Africa and noted the classes and types of errors that occurred in identification. I also used information from herbarium specimens and distribution data collected in the field to determine whether a species was introduced, naturalized and invasive. I found that 72% of the specimens were not named correctly. The inaccuracies were due to human error (70%) (misidentification, and improved identifications) and species identification problems, (30%) (synonyms arising from inclusion of *Callistemon* and unresolved taxonomy). At least 36 *Melaleuca* species have been introduced to South Africa, and field observations indicate that ten of these have naturalized, including five that are invasive. While most of the errors likely have negligible impact on management, I highlight one case (*M. parvistaminea*) where incorrect identification led to an initially inappropriate management approach and the initial error was propagated in later lists of invasive species. Invasive species lists need to be carefully reviewed to minimise errors, and herbarium specimens supported by DNA identification are required where identification using morphological features is particularly challenging.

Chapter 5. To improve prediction of which *Melaleuca* species could become naturalized or invasive I assessed a variety of traits for 36 *Melaleuca* species in South Africa. I collected information on traits that reflect species characteristics, biogeographic and human-usage patterns, and looked for predictors of invasiveness and naturalisation using generalised linear models. Residence time for *Melaleuca* species in South Africa is strongly positively correlated with naturalization, indicating that an invasion debt for the 27 non-naturalized species might exist. Native range size (using the convex-hull methodology) is not an important correlate for ability to naturalise or invasiveness. This indicates that stochastic factors like fire and finer scale habitat requirements may play a bigger role in invasion.

The thesis is a contribution to the study of model groups in invasion biology (Kueffer et al., 2013). The case studies for *M. parvistaminea* and *M. quinquenervia* highlighted the need for early detection and provided practical management guidelines and recommendations for the entire group. Chapter 4 contributed a specimen-based list of *Melaleuca* species present in South Africa that included information on the introduction status for each species. The need for accuracy in invasive species lists was also highlighted with recommendations as to how this could be addressed. The prediction of risk was informed by the traits analysis, emphasizing residence time as a key predictor, while also comparing and contrasting findings in previous studies. Thus this study combines elements informing the management of biological invasions while furthering current knowledge in the field.

Tesis opsomming

Die evaluering van moontlike indringerplante is 'n belangrike deel van die bestuur van indringerspesies. Verslae oor verskeie genaturaliseerde en indringer *Melaleuca*-spesies in Suid-Afrika het gelei tot 'n ondersoek rakende welke van hierdie spesies tans in die land is en watter van hierdie spesies 'n gevaar inhou. Ek het twee *Melaleuca*-spesies in Suid-Afrika, waarvan die aanvanklike indringergevaar-profiele verskil, evalueer (Hoofstukke 2 en 3); die indringerstatus van die *Melaleuca*-spesies wat in Suid-Afrika ingebring is, bepaal, en sodoende foute in taksonomiese identifikasie geïdentifiseer (Hoofstuk 4); en bepaal watter kenmerke dié groep se indringerstatus affekteer (Hoofstuk 5).

In Hoofstuk 2 dokumenteer en bepaal ek die bestuur-opsies vir die eerste aangetekende indringing van *Melaleuca parvistaminea* Byrnes (oorspronklik geïdentifiseer as *M. ericifolia*) in die wêreld, en in die konteks van 'n Suid-Afrikaanse vleiland-ekosisteem. 'n Ondersoek rakende waar hierdie spesie voorkom, dui aan dat die hele indringing beperk is tot drie lokaliteite tussen Tulbagh en Wolseley in die Wes-Kaap, en dat die bevolkings beperk is tot areas wat tans of voorheen bedek was deur denneplantasties (hoofsaaklik *Pinus radiata*). Om digtheid te bepaal, het ek 42% van die drie geïdentifiseerde areas ondersoek en ~26 000 plante verspreid oor 1800 ha (gekondenseerde blaremassa van 1.15 ha) gevind. Ten minste 63% van die aangetekende plante was kiemplantjies of onvolwasse, meestal minder as 4 jaar oud, en meeste van hulle het voorgekom in habitatte wat seisoenaal oorstroom (maar nie deurdrenk is nie). *Melaleuca parvistaminea* skep enkelspesie-stande wat die inheemse struikveld-plantegroei (Breede Skalie Renosterveld) oordek, dus word dit as 'n moontlike transformatorspesie geag. Die modellering van spesie-verspreiding het groot areas met geskikte klimaat in die Wes-Kaap geïdentifiseer, en gedui op die aansienlike moontlikheid vir indringing van die spesies van Suid-Afrika. Die afkap van plante veroorsaak die verspreiding van sade uit die laatbloeiende saadhuisies, en dit lei tot die oorvloedige aanwas van kiemplantjies na die winterreën (tot en met ~18 000 kiemplantjies per m²). Geen bewyse van 'n ondergrondse saadbedding is gevind nie. Nadat die plante afgesny is op grondvlak of met onkruiddoder behandel is nadat hul gesny is, het dit nie weer uitgeloop nie. Die indringerbevolkings van hierdie water-verspreide spesie is naby hoof riviere (Berg en Breede), maar die omliggende platteland is grotendeels verander en nie geskik vir vestiging nie. 'n Groot gedeelte van die area laer af langs die rivier vanwaar die indringing is, is oop plantegroei wat nie geskik is vir groot aanwas nie; hierdie area sal maklik wees om te ondersoek en dit sal dus maklik wees om klein/jong plantjies te vind. Gevolglik, alhoewel die mate van die indringing groot is (moontlik 9185 ha), kan die indringing afgebaken word met redelike sekerheid, en word uitroeiing as haalbaar geag aangesien saadjies vir ongeveer 'n jaar oorleef, kiemplantjies volle wasdom na 4 jaar bereik, en die spesie 'n saadskieter is. Indien mens die gevaar wat die indringers inhou in ag neem, word die uitroeiing van die indringers aanbeveel, en moet *M. parvistaminea* gelys word as 'n kategorie 1A-indringer (wat verpligte beheer vereis) onder die voorgenome indringerspesies-regulasies van Suid-Afrika se Nasionale Omgewingsbestuur: Biodiversiteitswet (10/2004). Ek is van mening dat soek-en-vernietig aksies die spesie teen 2021 kan uitroei teen die volgende koste: ZAR 3 475 000 (US$ 355 400).

Hoofstuk 3. Die ontdekking van die genaturaliseerde bevolking van *Melaleuca quinquenervia* in Suid-Afrika in 2009 het genoodsaak dat ek 'n evaluering van hierdie spesie se verspreiding in Suid-Afrika doen. Ek het rekords gevind by sewe lokaliteite in twee van die nege provinsies van Suid-Afrika, met genaturaliseerde bevolkings in twee terreine – ~300 plante is ontdek op 0.3 ha van 'n gelokaliseerde moerasland teen 'n berghang, terwyl daar in 'n ou arboretum 12 groot aangeplante bome en nege genaturaliseerde bome gevind is. 'n Addisionele herbarium-rekord van Mosambiek beweer dat hierdie wêreldwye indringer teenwoordig is op ander terreine binne die substreek. Dit beteken dat, alhoewel die uitroeiing van die spesie in Suid-Afrika aanbeveel word (en as moontlik geag word), verdere werk vereis word om die status van die spesie vas te stel en om te evalueer of uitroeiing van die spesie in die substreek moontlik is.

Hoofstuk 4. Lyste van ingevoerde spesies voorsien noodsaaklike agtergrondinligting ten opsigte van die bestuur van, en navorsing op biologiese indringings. Die samestelling van hierdie lyste is ongelukkig geneig om

’n verskeidenheid foute te bevat. Ek beklemtoon die gereeldheid en gevolge van sulke foute deur die genaturaliseerde *Melaleuca*-spesies (sensu lato, insluitend *Callistemon*) in Suid-Afrika as ’n gevallestudie te gebruik. Ek het 111 herbarium-rekords van Suid-Afrika gebruik en die klasse en tipes foute genoteer wat in die identifikasie voorgekom het. Ek het ook die inligting van die herbarium-rekords en die verspreidingsdata wat in die veld versamel is, gebruik om vas te stel of ’n spesie ingevoer, genaturaliseerd of ’n indringer was. Ek het gevind dat 72% van die rekords foutief benoem is weens menslike foute (70%) (verkeerdelike identifikasies, en as gevolg van taksonomiese naamsveranderinge) en spesie-idenfikasiefoute (30%) (sinonieme wat ontstaan het weens die insluiting van *Callistemon* en onopgeloste taksonomie). Ten minste 36 *Melaleuca*-spesies is ingevoer na Suid-Afrika en veld-waarnemings dui daarop dat tien van hierdie spesies hulself genaturaliseer het, insluitend vyf wat tans as indringerplante geag word. Alhoewel meeste van die foute moontlik ’n geringe impak op bestuur het, beklemtoon ek een saak waar foutiewe identifikasie gelei het tot die onvanpaste bestuursbenadering daarvan, asook sommige voorbeelde van foute in gepubliseerde lyste. Indringerspesielyste moet sorgvuldig nagegaan word om foute uit te skakel, en in gevalle waar identifikasie bemoeilik word deur morfologiese kenmerke, word dit vereis dat herbarium-rekords ondersteun word deur DNA-identifikasie.

Hoofstuk 5. Om die voorspelbaarheid van watter *Melaleuca*-spesies moontlik genaturaliseerd of indringers kan word, meer akkuraat te maak, het ek ’n verskeidenheid kenmerke van 36 *Melaleuca*-spesies in Suid-Afrika geassesseer. Ek het inligting versamel rakende kenmerke wat die spesie se karakter-eienskappe, biogeografiese- en mensverbruikerspatrone reflekteer, en algemene liniêre modelle gebruik om te soek vir voorspellers van indringerskap en naturalisering. Die bestaanstydperk van die *Melaleuca*-spesies in Suid-Afrika is baie sterk verwant aan die tydperk van naturalisering, wat daarop dui dat ’n moontlikheid van indringing vir 27 van die nie-genaturaliseerde spesies kan bestaan. Die omvang van natuurlike verspreiding (met die gebruik van die “convex-hull” metode) is nie ’n belangrike korrelaat vir die vermoë van die spesie om genaturaliseerd te word of ’n indringer te wees nie. Dit dui daarop dat stogastiese faktore soos brande en spesiale habitat-vereistes ’n groter rol kan speel rakende die indringerstatus van die spesie.

Hierdie tesis dra by tot die studie van voorbeeldgroepe in indringerbiologie (Kueffer et al., 2013). Die gevallestudies van *M. parvistaminea* en *M. quinquenervia* het die behoefte aan vroegtydige ontdekking beklemtoon en praktiese bestuursriglyne en aanbevelings vir die hele groep voorsien. Hoofstuk 4 het bygedra tot ’n rekord-gebaseerde lys van die *Melaleuca*-spesies wat in Suid-Afrika teenwoordig is, en het ook inligting ingesluit rakende die invoerstatus van elke spesie. Die behoefte aan die akkuraatheid van indringerspesielyste is ook beklemtoon, met aanbevelings van hoe dit aangespreek kan word. Die risiko-voorspelling is beïnvloed deur die kenmerk-ontleding, en dit het die bestaantydperk as ’n belangrike faktor beklemtoon en die bevindinge van vorige studies met mekaar vergelyk. Hierdie studie kombineer dus die elemente wat die bestuur van biologiese indringings beïnvloed, en verbreed die huidige kennis in hierdie veld.

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For further details see acknowledgments under chapter 2 to chapter 5.

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Chapter 1: Introduction

Patterns in tree invasions are reasonably well understood for some taxonomic groups, but poorly understood in others (Richardson, 2006; Richardson et al., 2011). Adequate knowledge of these patterns (including introduction history, propagule pressure, spread over time and impact) allows for proper management and risk assessment while informing the prioritisation of species for control, by evaluating impact, feasibility of control and other factors. Evaluation of little known or recently invading taxa is crucial to early detection and eradication efforts. These assessments are a significant contribution to local and international strategies for managing invasive alien plant impacts (Wittenberg and Cock, 2001), and for furthering understanding of tree invasions (Richardson et al., 2011).

Pines, acacias and eucalypts are the most widely planted tree groups in regions outside their native ranges (Richardson et al., 2011). Some invasive plant taxa, like pines and Australian acacias, are model groups for studying the dynamics associated with tree invasions (Richardson, 2006; Richardson et al., 2011). Large numbers of taxa in these groups provide sufficient variety of situations to glean generalisations that have been hard to come by in invasion biology (Elliott-Graves, 2016). Generalizations for predicting invasiveness are tentative, perhaps because many other plant groups have not yet been studied in a taxon-specific manner. This is why research priorities identified by Richardson and Rejmánek's (2011) global review of invasive trees and shrubs include the identification of invasive potential in large plant groups (families or genera) or in taxa likely to be transported. The Myrtaceae is a large family (~ 6 000 species) with 35 species recorded as invasive (Rejmánek and Richardson, 2013) and is therefore a prime candidate for investigation to further our understanding of invasion biology.

Although transportation of eucalypts (the most speciose group in Myrtaceae) across the globe has been similar in magnitude and timing to movements of pines and acacias, eucalypts are much less successful as invasive species. Rejmánek and Richardson (2011) speculate that possible causes of the limited invasiveness in the group include poor seed dispersal, high seedling mortality, and absence of compatible ectomycorrhizal fungi. Eucalypts belong to a group of dry-seeded species in the family Myrtaceae, in the historically recognised subfamily, Leptospermoideae. Thirty-five species in the family Myrtaceae are reported as invasive globally, of which nine are eucalypts (Rejmánek and Richardson, 2013). Most of these invasions have not yet reached proportions where impacts are very noticeable (Le Maitre et al., 2002; Richardson and Rejmánek, 2011), although Le Maitre et al. (2002) measured significant reduction of water availability in areas invaded by *Eucalyptus* species in South Africa.

Invasions by other tree groups, more recently introduced, along different pathways, e.g. horticulture, biofuels, are becoming prominent (Moodley et al., 2013; Jacobs et al., 2014). *Melaleuca* and *Callistemon* (now partially subsumed within *Melaleuca* (Craven, 2006; Brophy et al., 2013)) are sister genera of *Eucalyptus* in the family Myrtaceae. Species in these genera have mainly been introduced and disseminated for ornamentation, but also for forestry (Brophy et al., 2013) and some have increasing pharmaceutical value (e.g. tea tree oil from *M. alternifolia*; Tripathi et al., 2011). Like Australian acacias and eucalypts, melaleucas are a speciose group (~ 290 species) of shrubs and trees primarily originating from Australia that have a long history of introductions to many parts of the world (Richardson and Rejmánek, 2011; Brophy et al., 2013). While many facets of the invasion ecology of acacias and eucalypts have been studied, e.g. native range size analyses for *Acacia* and *Eucalyptus* (Hui et al., 2011, 2014), few studies have addressed the invasion ecology of *Melaleuca* species (except for *M. quinquenervia*). The smaller scale of invasions could be a reflection of introduction history (shorter residence time and lower propagule pressure (Richardson and Rejmánek, 2011)), but general traits associated with invasiveness could also play a role in reflecting these patterns. As such, the genus *Melaleuca* provides an interesting comparison to eucalypts, pines, and acacias.

Although 27 *Melaleuca* species are listed the Global Compendium of Weeds (Randall, 2007), the invasive status (sensu Richardson et al., 2000) of most taxa is debatable, and none except *M. quinquenervia* are known to cause major impacts (Dray et al., 2006). *Melaleuca quinquenervia* is a notorious invader in the Florida Everglades, USA, where large numbers of propagules were deliberately introduced over a wide area (Serbesoff-King, 2003), it is also listed among 100 of the world's worst invaders (Lowe et al., 2000). This also provides a reason that the invasion risk of other taxa in the genus should be assessed.

In South Africa, 16 *Callistemon* and 27 *Melaleuca* species are known to be cultivated (Glen, 2002), although none are recorded in Poynton's (2009) volume on tree planting in South Africa. Three species of *Callistemon* and eight *Melaleuca* species are listed in the South Africa Plant Invaders Atlas (SAPIA), indicating some degree of naturalization and perhaps invasive potential (Henderson, 1998; van Wyk et al., 2012; Wilson et al., 2013). Thus, an evaluation of this entire genus in South Africa would offer a significant contribution to our understanding of tree invasions.

A number of *Melaleuca* species are currently receiving attention as potential invasive species in South Africa. *Melaleuca parvistaminea* and *M. quinquenervia* are two notable examples that have naturalised in the Tulbagh/Wolseley area of the Western Cape province, near the Kluitjieskraal forestry station. These species are the focus of SANBI Invasive Species Programme projects (van Wyk et al., 2012; Wilson et al., 2013). Initially the perception of risk for *M. quinquenervia* was very high because of its history of invasiveness elsewhere (Serbesoff-King, 2003), while the lesser known *M. parvistaminea* was generally deemed to pose a lower risk. In chapter 2, I discuss the status of *M. parvistaminea* as an invasive species and assess whether eradication is a feasible and desirable management goal for this species. In chapter 3, I detail the distribution of *M. quinquenervia* in South Africa. However, many other species besides these two were used in forestry trials (Gibbs, 1998), horticulture or have been introduced to arboreta. In addition, records have been found on the iSpot website (http://www.ispot.org.za/) and on the SAPIA database.

Accuracy in invasive species listing is important as these lists are used widely as a tool to manage problematic species. McGeoch et al. (2012) discuss the types of uncertainties and errors that can occur in the listing process and suggests a framework for categorising these errors. In the attempt to compile a comprehensive list of *Melaleuca* species in South Africa (and determine their invasive status), I discovered errors in identification of herbarium specimens. This prompted an evaluation of the types and rates of errors for identification. In chapter 4 I discuss how this affects invasive species lists, while reporting on the invasive status for *Melaleuca* in South Africa.

A key challenge in invasion biology has been to identify which traits make some alien species invasive or more invasive than others. Studying model groups has produced much knowledge on this question and has yielded invaluable information as natural experiments (Richardson, 2006; Kueffer et al., 2013). Of the tree genera that were widely disseminated across the world, pines and Australian acacias have emerged as model groups for elucidating key features of tree invasions (Richardson, 2006; Richardson et al., 2011). In chapter 5 I explore the traits that may be associated with naturalisation and invasion in South Africa and which may be used to evaluate invasion risk in the group.

Chapter 6 includes a general discussion, summarising and drawing together elements of the thesis. Recommendations are made for the prediction of invasion risk in *Melaleuca* and the implications for management are discussed. I also discuss how the findings of this thesis fits in with current knowledge of invasive tree groups and suggest further work that should be undertaken.

The aims of the thesis were to:

- Provide management case studies for two species and assess their risk in South Africa (Chapter 2 and 3);
- Determine which species are naturalised and invasive in the group (Chapter 4);
- Highlight errors in herbarium specimen identification that can affect invasive species listing (Chapter 4);
- Determine which traits are associated with naturalisation and invasion success (Chapter 5); and
- Develop general recommendations for management of this group (Chapter 2, 3 and 6).

Chapter 2: *Melaleuca parvistaminea* Byrnes (Myrtaceae) in South Africa: Invasion risk and feasibility of eradication

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Author contributions:

LEOJ, DMR, JRUW: Planned the study

LEOJ: Collected data, did all statistical analyses and wrote the first draft of the paper

DMR, JRUW: Edited the manuscript

JRW: Provided guidance on statistical analyses and bioclimatic modelling

A part of the work reported in this chapter was done in partial fulfilment of my BSc Hons degree that was completed by Dec 2012. The contribution towards this MSc includes additional surveys including all the delimitation survey-work, the development of eradication and management strategy, and improved analyses. This was a core part of the first year of my MSc, with the manuscript only submitted to the journal by Nov 2013. The table detailing the differences between *Melaleuca ericifolia* and *M. parvistaminea* and discussion on misidentification was included as supplementary material. Time to eradication and cost estimates were revised. Delimitation surveys were conducted and using GIS a map indicating different management strategies, taking land-use into consideration, was compiled. Distribution and infestation area estimates were improved as a result of collecting an additional ~13 000 coordinates and associated data.

Abstract

We document and assess management options for the first reported invasion of *Melaleuca parvistaminea* Byrnes (initially identified as *M. ericifolia*) in the world, in the context of a South African wetland ecosystem. Delimitation surveys indicate that the entire invasion is restricted to three sites between Tulbagh and Wolseley and that populations are only associated with areas currently or previously covered by pine plantations (primarily *Pinus radiata*). To estimate abundance we surveyed 42% of the three identified areas and found ~26,000 plants over 1800 ha (condensed canopy area of 1.15 ha). At least 63% of recorded plants were seedlings or juveniles, mostly <4 years old, and most occurred in seasonally inundated (but not waterlogged) habitats. *Melaleuca parvistaminea* creates monospecific stands that overtop the native shrubland vegetation (Breede Shale Renosterveld) and is thus considered a potential transformer species. Species distribution modelling also revealed large areas of climatically suitable habitat in the Western Cape, pointing to substantial invasion debt for the species in South Africa. Felling triggers seed release from serotinous capsules, resulting in prolific seedling recruitment after winter rains (up to ~18,000 seedlings/m2). No evidence of a soil-stored seed bank was found, and when plants are cut at ground level or treated with herbicide after cutting, plants do not resprout. The invasive populations of this water dispersed species are close to major rivers (the Berg and Breede), but the intervening countryside is largely transformed and is unfavourable for establishment. Much of the area downstream from the invaded area is open vegetation that is unsuitable for major recruitment but easy to survey and detect small plants. Consequently, although the extent of invasion is large (potentially 9185 ha), the invasion can be delimited with some confidence, and eradication is considered achievable since seeds only survive for about a year, seedlings achieve maturity after 4 years, and because the species is an obligate reseeder. Given the threats posed, eradication is desirable and *M. parvistaminea* should be listed as a category-1a invader (requiring compulsory control) under the proposed invasive species regulations under South Africa's National Environmental Management: Biodiversity Act (10/2004).We estimate that search and destroy operations could eradicate the species by 2021 at a cost of ZAR 3 475 000 (US$ 355 400).

Keywords: Biological invasions; Early detection; Eradication; Invasive plants; Myrtaceae; Tree invasions

2.1 Introduction

Tree species have been introduced to South Africa for many reasons, including forestry and horticulture (Richardson et al., 2003; Richardson and Rejmánek, 2011). Many species of *Acacia* and *Eucalyptus* from Australia, and *Pinus* species from the Northern Hemisphere were introduced to supply timber, to bind dunes and to provide fire wood. Many of these species have become invasive, their success partly facilitated by the same traits for which they were imported, such as fast growth, and the capacity to fix atmospheric nitrogen (Richardson, 1998; Castro-Díez et al., 2011). The distribution and spatial extent of such invasions are strongly correlated with the extent of planting (Wilson et al., 2011; Procheş et al., 2012) and residence time (Wilson et al., 2007), suggesting that the extent of invasions is more strongly influenced by the extent and timing of human usage than by particular traits of the species (McGregor et al., 2012). If this is the case, many species introduced to only a few sites and which still have relatively small invasive ranges, pose a substantial threat to ecosystems if they are allowed to spread and/or to be disseminated further by humans (see also Donaldson et al., 2014a, 2014b). The concept of “invasion debt” (Essl et al., 2011) posits that even if introductions cease (and/or other drivers of invasion are relaxed, e.g., propagule pressure is reduced), new invasions will continue to emerge and already-invasive species will continue to spread and cause potentially greater impacts, since large numbers of alien species are already present, many of them in a lag phase. Cognizance of these factors is particularly important where introduced species have been historically planted in low numbers at a few sites, but then not subsequently managed and left to invade unchecked (Wilson et al., 2013), but, such species are also often suitable targets for eradication (Zenni et al., 2009; Kaplan et al., 2012, 2014). The Invasive Species Programme of the South African National Biodiversity Institute is responsible for detecting such invasions and for evaluating whether eradication (i.e. total removal of all plants and propagules) is feasible (Wilson et al., 2013).

Thirty-four species in the family Myrtaceae are known to be invasive globally (Rejmánek and Richardson, 2013). Of these, some fleshy-fruited species (notably *Psidium, Eugenia* and *Syzygium* species) are used for food, *Eucalyptus* species are widely planted for forestry, and 24 species (including *Melaleuca* taxa) are widely used as ornamentals. Only one species in the genus *Melaleuca* has been recorded as causing major impacts as an invader to date. *Melaleuca quinquenervia* is a notorious invader in the Florida Everglades, USA (Serbesoff-King, 2003). Although 27 *Melaleuca* species are listed in the Global Compendium of Weeds (Randall, 2007), the invasive status (sensu Richardson et al., 2000) of most is questionable because they are only weedy or close to sites where they are considered native. *Melaleuca quinquenervia* has been recently detected in the wild in South Africa (van Wyk et al., 2012), prompting a re-evaluation of the state of all introduced *Melaleuca* species in South Africa.

It has been proposed that *Callistemon*, a sister genus, should be included in *Melaleuca* because characters upon which the separation of the two were previously based are continuous (Craven, 2006). Although recent analyses using molecular and morphological data support the inclusion of *Callistemon* within *Melaleuca* (Edwards et al., 2010), some Australian state herbaria still recognise *Callistemon* as a separate taxon (Udovicic and Spencer, 2012). Many species of *Melaleuca* and *Callistemon* have been moved widely around the world only fairly recently. Many are traded in horticulture (Richardson and Rejmánek, 2011) and some also have major pharmaceutical value (e.g. tea tree oil from *M. alternifolia*; Tripathi et al., 2011). In South Africa, 16 *Callistemon* and 27 *Melaleuca* species are known to be cultivated (Glen, 2002). Although no *Callistemon* or *Melaleuca* taxa are listed in Poynton's (2009) book "Tree planting in Southern Africa: vol. 3 Other Genera", three *Callistemon* and eight *Melaleuca* species are listed in the Southern African Plant Invaders Atlas, indicating a degree of naturalisation or invasion (Henderson, 1998; van Wyk et al., 2012; Wilson et al., 2013). One *Callistemon* species (*C. rigidus = M. linearis var. linearis*) was listed as an "emerging invader" in an analysis that prioritized alien plant species and areas for management action in South Africa (Nel et al., 2004).

Melaleuca quinquenervia was found naturalised at two sites in the Western Cape (Wilson et al., 2013). At one of these sites a far larger invasion of another species, *M. parvistaminea,* was found. The last-mentioned species is not known to be invasive anywhere in the world (Rejmánek and Richardson, 2013). Initial work on *Melaleuca* in South Africa by the Invasive Species Programme focussed on *M. quinquenervia* because of its prominence as an invasive plant in Florida and therefore its perceived high-risk status in South Africa. *Melaleuca parvistaminea* is however currently much more widespread and is currently having a much greater impact on the local environment than *M. quinquenervia* (van Wyk et al., 2012).

This study aims to: a) determine the risk posed by *M. parvistaminea* as an invasive species in South Africa (this being the first record of invasiveness anywhere in the world); b) assess the current national-scale distribution and population dynamics at the known sites of invasion; and c) develop recommendations for management, and specifically to determine whether eradication is feasible.

2.2 Materials and Methods

2.2.1 Study species

Melaleuca parvistaminea is a small tree or shrub up to 4 m tall, native to New South Wales and Victoria in Australia (Albrecht, 1987). It has whitish, bottle-brush like flowers (Fig. 2.1) with conspicuous stamens typical of many species in the genus and to some extent, the family Myrtaceae. Flowering occurs only from September to November. The species was found to be naturalised in the Western Cape province of South Africa during routine conservation management inspections in the spring of 2007. It was identified as a problematic species, as it had already formed monospecific stands (Fig 2.1). The species was initially identified as *M. ericifolia,* but was later found to be *M. parvistaminea,* a close relative (see S2.1 for discussion on species identification).

Fig. 2.1. *Melaleuca parvistaminea* invasions in the Tulbagh-Wolseley area, South Africa, A) multi-stemmed seedling, B) whitish bottlebrush-like flowers, C) pinkish petals on flower buds, D) seed release one week after cutting a twig, E) post-fire recruitment in wet areas in August 2012, F) serotinous seed capsules on branches, G) virtually monospecific stands of *M. parvistaminea* overtopping native vegetation, and H) profuse seedling recruitment near burnt adult trees

Although *Melaleuca parvistaminea* is reported as an environmental weed in Australia in the Global Compendium of Weeds (Randall, 2007), this record from SE Australia is likely within its native range (S2.2); and so does not qualify as invasive under the biogeographic definition of Richardson et al. (2000). The occurrence of *M. parvistaminea* in South Africa is therefore the first record of invasiveness (sensu Richardson et al., 2000) anywhere in the world.

2.2.2 Study site

The three known localities of *M. parvistaminea* in South Africa are in a narrow area between the towns of Tulbagh and Wolseley in the Western Cape (Fig. 2.2b; Table 2.1). The area is situated between the slopes of the Waterval Mountains and the cultivated lowlands of the Upper Breede River valley. Before 2000, most of this area was managed solely by forestry companies but since then parts of the area are in transition from pine plantation to nature conservation, following the recent exit strategy for commercial forestry in the region (Louw, 2006). The remaining plantation (and some of the areas no longer under forestry) is subdivided into management blocks (~300 m x 300 m) separated by gravel roads; which made the management of the survey easier (Fig. 2d). A nursery is situated near the Kluitjieskraal forestry station, and several *Melaleuca* species have naturalised in the area, though *M. parvistaminea* is by far the most widespread of these (van Wyk et al., 2012).

Table 2.1
Summary of characteristics and management of *Melaleuca parvistaminea* at three sites in the Tulbagh-Wolseley area in the Western Cape, South Africa. The natural vegetation type at all sites is Breede Shale Renosterveld (Mucina and Rutherford, 2006). The species was introduced for used as an ornamental plant or for windbreaks before 1990 at all three sites. Fig. 2.2b shows a map of the sites with the landscape.

	Kluitjieskraal plantation	*Kluitjieskraal wetland*	*Waterval*
Location	S 33.3872° E 19.1526°	S 33.3872° E 19.1520°	S 33.3410° E 19.1158°
Size of area	1392 ha	538 ha	294 ha
Previous land use (before 2000)	Pine plantation	Pine plantation	Pine and eucalypt plantation
Current land use	Mainly pine plantation	Conservation (wetland rehabilitation)	Conservation
Local authority	MTO Forestry	MTO Forestry	CapeNature
Record present in SAPIA database before project initiation	No	Yes	No

Since the first report of the invasion in 2009 at the Waterval site, the extent of *M. parvistaminea* has been estimated by gaining insights from land managers and active walked surveys following the approach taken by

Kaplan et al. (2014). In the Kluitjieskraal plantation and wetland (Fig. 2.2b, d) an ex-forester in the area knew where many of the sites of invasion were (indicated on Fig. 2.2b) although he was previously unaware that the species was a non-native *Melaleuca*. While these records served as a very valuable starting point for surveys (cf. Kaplan, 2012; Kaplan et al., 2014), all blocks were regarded as potentially invaded.

The Kluitjieskraal Wetland (Fig. 2.2b) is being rehabilitated by the Working on Wetlands programme and was also previously covered by *Pinus radiata*. The Kluitjieskraal wetland is characterised by seasonally and permanently wet areas. As part of wetland rehabilitation efforts, clearing of major invaders took place prior to this study, but no evidence of previous *M. parvistaminea* clearing was found. A clearing contract (220 ha), which aimed to clear *M. parvistaminea* plants and to collect data, was initiated by SANBI's Invasive Species Programme at this site in April 2012 (Fig. 2.2e).

The Waterval site (Fig. 2.2c), in an area designated as a "forestry exit" zone – areas identified as being unsuitable for sustainable commercial forestry as part of a national forestry strategy. Pine plantations in the area (as well as invasive species – notably Australian acacias and eucalypts) are being cleared, the aim being to restore the natural fynbos vegetation. The area has been managed by the provincial conservation authority (CapeNature) since 2000 (Table 2.1) (Nagan, 2008). Despite the clearing of major invaders in the area, *M. parvistaminea* was allowed to persist, almost certainly because it was mistaken for a native species. Some data collection and initial clearing took place at this site before it burnt in January 2012.

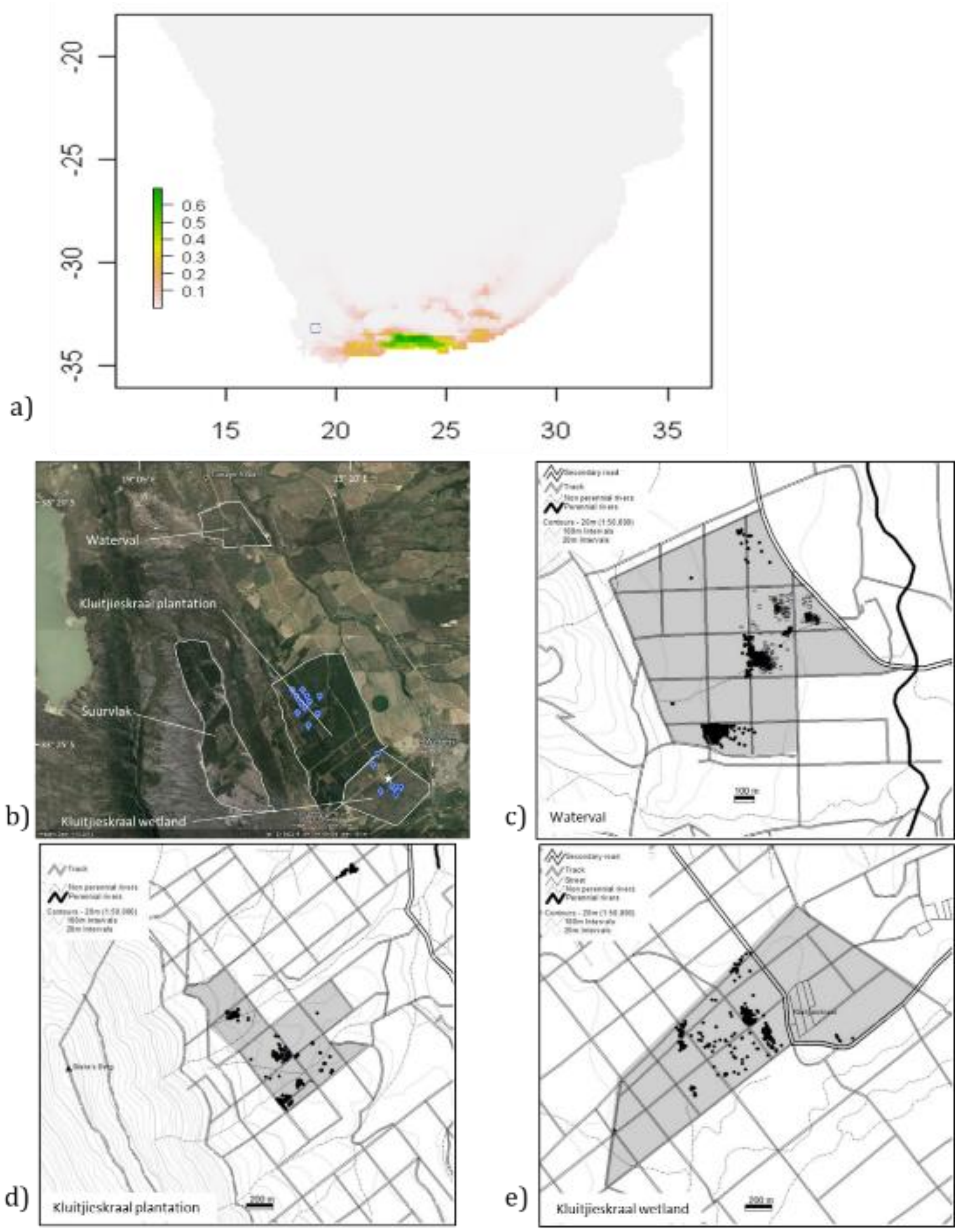

Fig. 2.2. *Melaleuca parvistaminea* invasion in the Western Cape, South Africa: a) bioclimatically suitable areas (green shading indicates most suitable areas) predicted for *Melaleuca parvistaminea* in South Africa (the open square indicates the study area), AUC=0.998 using MaxEnt presence-only modelling; b) survey sites in the Tulbagh-Wolseley area (Table 2.1), with *Melaleuca parvistaminea* presence localities (blue icons) identified by a local forester. The Kluitjieskraal forestry station and nursery are indicated by the star; c) Waterval, open squares indicate data collected before the January 2012 fire; d) Kluitjieskraal plantation; and e) Kluitjieskraal wetland. Solid circles represent burnt plants at Waterval (c), but represent live plant data at Kluitjieskraal plantation and Kluitjieskraal wetland (d, e) collected during this study. At the three sites (c-e), grey shading indicates surveyed area and at Kluitjieskraal wetland shading also indicates the clearing contract area.

2.2.3 Delimiting the extent of M. parvistaminea *in South Africa: national, regional, and local surveys*

When attempting eradication, delimiting the extent of the invasion is a crucial factor for success (Panetta and Lawes, 2005). To determine whether any other localities of *M. parvistaminea* existed in South Africa, tree planting records, the iSpot website (http://www.ispot.org.za/) and herbarium specimens were examined, and numerous botanists and foresters were consulted. Pamphlets (S2.5) with contact information, pictures and a description of *M. parvistaminea* were distributed to land managers within the region known to be the focus of planting activities. As part of the regional-scale delimitation strategy, CapeNature and MTO forestry staff assisted as "spotters" for the species throughout the area. Besides the study sites, suitable sites for *M. parvistaminea* were determined by including likely areas of dispersal and establishment, while excluding unsuitable areas based on unlikely habitat type and cultivated or urban areas. The exclusion of areas were based on observations thus far, to restrict the local survey area to a practically achievable size. The national and regional survey approaches were intended to provide detection of plants in the exclusion and as yet unknown areas.

Each sites identified as invaded by the local forester in the Kluitjieskraal plantation, was systematically surveyed by walking parallel transects (Fig. 2.2d). To ensure thorough surveying and to provide evidence of the surveyed area, a track of the walked transects and waypoints of plants were taken with a handheld GPS (Garmin GPSmap 60CSx) (e.g. Zenni et al., 2009; Kaplan et al., 2012). No tracks were taken at the Waterval and Kluitjieskraal wetland sites as these data were collected prior to or independently of this study.

To estimate the population dynamics and size of the invasion, all plants were counted and ~5000 were measured. Plant height, canopy width, stem diameter and evidence of reproduction (presence of seed capsules and/or flower buds) were recorded. Due to time constraints, midway through data collection, it was decided to prioritise survey effort. Thereafter, plants were counted and only the geographic position was recorded. To assess age and size at reproduction, two 50 x 50 m plots (1 dry site, 1 wet site) were selected in a densely invaded area (>100 individuals per plot) that contained both seedlings and adults to ensure size and age range over a reasonable sample size. To do this, stumps were cut as close to the ground as possible and the age rings were counted in addition to the measurements described above. Since not all plants were aged, we attempted to find a relationship between physical measurements and plant age. The primary aim was to determine the size at which *M. parvistaminea* plants reach reproductive maturity and to inform monitoring protocols for the species.

At the Waterval site, distribution and plant allometric data were collected during 2009 and 2010. We surveyed the remaining population after the fire in January 2012 by counting and measuring burnt skeletons. Burnt individuals could only be identified where capsules were present (where these were absent *M. parvistaminea* skeletons could not be distinguished from several native shrub species); abundance is therefore likely to be underestimated. Only plant height, canopy width and stem diameter were measured at the Kluitjieskraal wetland by clearing contractors.

The extent of occurrence at each site was determined by calculating the area of a convex hull drawn around the most outlying points within each population. Condensed canopy, i.e. fine-scale area of occupancy, was calculated by adding a buffer equal to the canopy width per plant to each point, then by summing the area contained with each buffered point (Wilson et al., 2014a). These spatial analyses and maps were produced in ArcGIS 10 (ESRI, 2011); statistical analyses were conducted in R (R Development Core Team, 2012).

2.2.4 Risk assessment and bioclimatic modelling

To collate information, determine invasive potential and identify areas requiring more research, the Australian Weed Risk assessment scheme (Pheloung et al., 1999) was used. This scheme has been applied in a variety of geographies and is reported to be consistently accurate (Gordon et al., 2008, 2010; Hulme, 2012). It also provides a standard method for collating information on potential impacts. The qualitative level of threat was also evaluated by determining by a) whether the species could over-top native vegetation; and b) whether it had (or could have) the properties of a transformer species (Wilson et al., 2014a).

To determine which areas are climatically suitable and therefore at risk of invasion by *M. parvistaminea* in South Africa, we modelled the climate niche using the algorithm MaxEnt 3.3.2 (Phillips et al., 2006). Presence data were downloaded from the Atlas for Living Australia (http://www.ala.org.au) and the Global Biodiversity Information Facility (http://data.gbif.org). Points outside the reported native range in Australia, duplicate records, points with accuracy greater than 1 km (including coordinates with two decimals or less where accuracy was not specified) and points in the ocean were removed manually. We aimed to verify climatic suitability (and not potential distribution in South Africa), therefore points in South Africa were also excluded. The bioclimatic variables were obtained from the WORLDCLIM dataset (www.worldclim.org) at 10 min resolution. The least inter-correlated variables included in the model were: isothermality, mean temperature of the driest quarter, mean temperature of the warmest quarter, precipitation seasonality and precipitation during the wettest quarter. For model verification, we report the area under the curve (AUC) statistic.

2.2.5 Post-clearing efficacy and post-fire recruitment

The reseeding habit of many serotinous species is characterised by adult mortality after fire which leads to seed-release from woody storage structures. This is then followed by profuse seedling recruitment in the low competition post-fire environment (Lamont et al., 1991). Post-fire recruitment at the Waterval site (burned in January 2012), was evaluated using a transect through a population of burnt adults. Adult survival after fire was also noted. Seedlings were counted in 1 x 1 m quadrats (centre positioned on the line) at 1-m intervals along the length of the transect, using a combination of actual counts and estimation based on coverage.

Plants were cleared immediately after data collection at the Waterval site in 2009 and 2010. The only other targeted clearing to date was in a subsection of the Kluitjieskraal wetland during April and May 2012 (the shaded area in Fig. 2.2e). Field observations at the Waterval site during 2010 informed clearing recommendations for the Kluitjieskraal wetland contract, thus providing an opportunity to evaluate post-clearing regeneration and the success of clearing operations. At the contract site, workers were asked to stack dead material (with seed capsules attached) in large piles (~25 m^2) in dry areas to minimize the area over which recruitment (seeds require seasonally waterlogged soils for germination) would take place and also to minimize the search area during follow ups. After winter (and seasonal rains), we specifically checked for adult plants that had been missed during clearing, seedling recruitment beneath and around stacked dead material, seedling recruitment around cut stumps, resprouting after cutting and herbicide application and for dead material not stacked on a pile or in wet areas.

Indiscriminate clearing of *M. parvistaminea* has however taken place at the Kluitjieskraal plantation. Brush-cutting of trees and shrubs around pine trees was part of routine plantation maintenance, and cut stumps were not painted with herbicides (as per standard protocols). This allowed us to observe the effects of this practice on recruitment and clearing efficacy. .

2.2.6 Estimate of cost for eradication

To determine the cost of eradication we extrapolated the costs of surveys, the clearing contract and the size of the surveyed and cleared to the total area. Using this information we estimated the total cost to achieve eradication (removal of all plants in the study area). Cost until eradication also included the amounts needed for surveying all likely areas (including delimitation surveys) before clearing. Follow-up costs were also projected using information on reproductive age and seed storage to determine the timing and frequency of follow ups. Time was measured in person days (number of days x number of people per day).

2.3 Results

2.3.1 National and regional survey

The population in the Tulbagh-Wolseley area is the only one we could confirm in the country. No additional records for *M. parvistaminea* were discovered via pamphlet distribution, surveillance by “spotters”, iSpot records and herbarium specimens in 2012. This species is not listed in any tree planting records nor is it being cultivated as an ornamental, suggesting that no populations exist outside of the Tulbagh-Wolseley area. Our observations with delimitation surveys in and around the three sites indicated that *M. parvistaminea* is only in the plantation areas in the vicinity of Kluitjieskraal.

An additional locality was reported by a contractor working at the Suurvlak plantation (indicated in Fig. 2.2b and in Fig. 2.4 as “unconfirmed report”). To verify this, we drove along gravel tracks through the plantation in suitable areas but failed to find any plants. Detectability was high in most areas because this area also burnt in January 2012. It is therefore likely that large, highly visible plants were destroyed in the fire or that this record is erroneous.

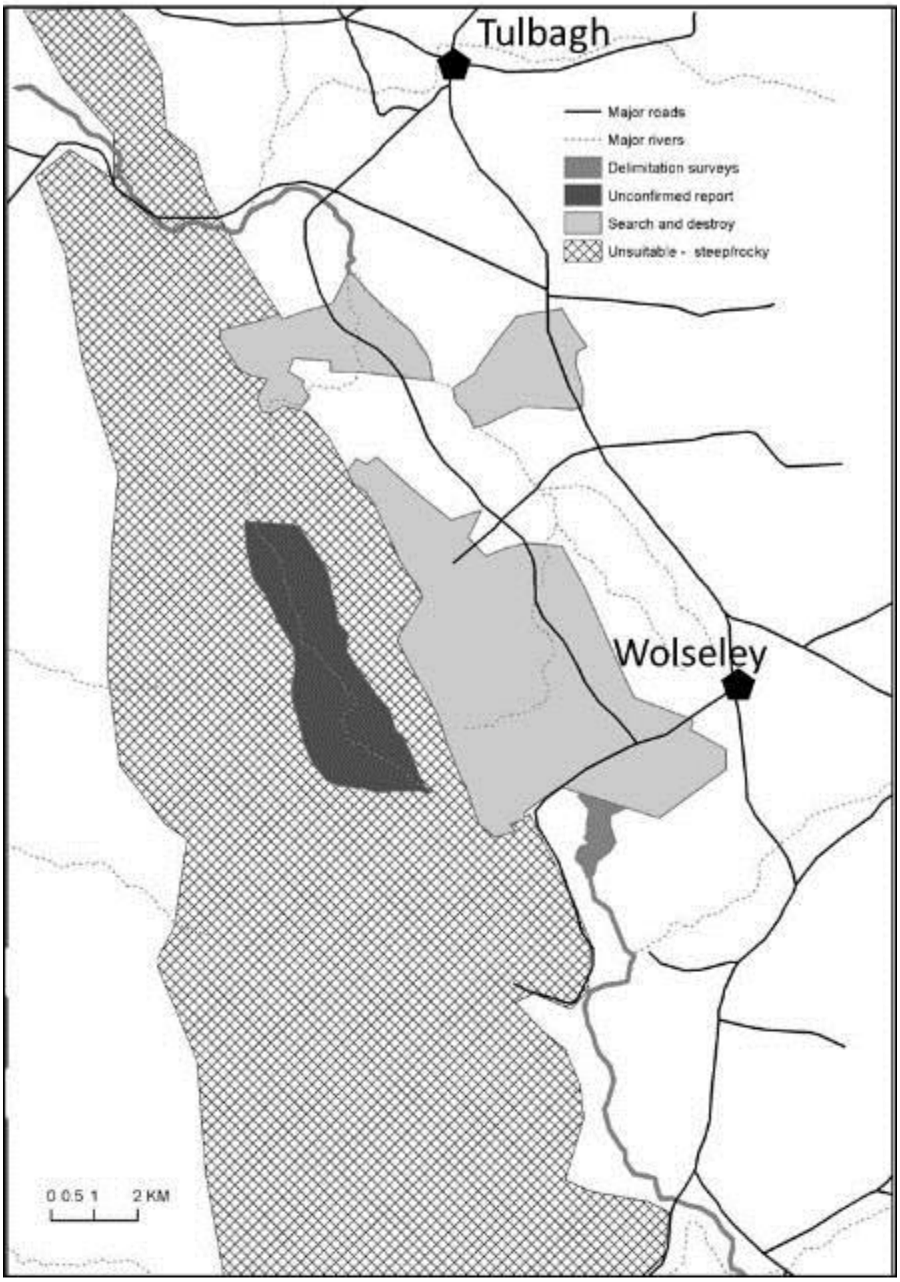

Fig. 2.4. Different management strategies that should be implemented in areas across the landscape. These strategies are: search and destroy in suitable and likely habitat, delimitation surveys that were undertaken along likely dispersal routes, i.e. streams, and during flowering time scanning an area where a report remains unconfirmed. Areas deemed unsuitable for *M. parvistaminea* on the basis of habitat are also indicated, and will therefore not be surveyed. Cultivated and urban areas are also unsuitable; these are indicated as white areas on the map.

2.3.2 Local delimitation and population dynamics

372 ha (42% of all areas earmarked for surveying) have been surveyed to date, including all areas identified by the forester at Kluitjieskraal plantation (Fig. 2.2b). A total of 26 302 plants (condensed canopy area of 1.15 ha) were recorded at the Waterval, Kluitjieskraal plantation and Kluitjieskraal wetland sites (Fig. 2c, d, e). For data where presence/absence of reproductive structures were recorded, 37% of plants were mature; the remainder were seedlings or juvenile plants. At Waterval, a total of 6629 plants were recorded. During 2009 and 2010,

2074 plants were recorded and measured. In 2012, the remainder of the population was surveyed after the January 2012 fire. We counted 3805 burned trees which is an underestimate of the actual numbers before the fire. Burnt trees were difficult to identify when seed capsules were absent, while no evidence remained of juvenile plants and seedlings after the fire. Regular Cape Nature patrols and our observations at the Waterval site suggest that it is unlikely that any unburned adult plants are present.

Abundance varied hugely between management blocks (range = 0-14863 plants), which made survey planning unpredictable and difficult, and also to determine the source of the invasive populations. Survey and clearing contracts will be issued by SANBI’s ISP to address the remaining area. Approximately 20 300 plants were recorded at Kluitjieskraal plantation over 58 ha.

The clearing contract at Kluitjieskraal wetland (Fig. 2.2e) surveyed and cleared 220 ha during April and May 2012 (292 person days), which contained 1822 plants. Therefore 318 ha must still be surveyed, potentially containing 2634 plants (assuming that densities are at same at this site).

The strongest correlation was found between age and log maximum height (Pearson's correlation co-efficient between age and maximum height ($r = 0.64$), average height ($r = 0.33$), stem diameter ($r=0.52$) and canopy width ($r=0.33$). Using a linear regression model, maximum height was used to predict the age of individual plants (and so of the various invasive populations).

Plants bear seeds at age 3–5 years, and 40% of plants carry seeds at four years (Fig. 2.3). Small plants (stem diameters < 1 cm) were difficult to age, and therefore ages of mature plants that were three years or less were possibly underestimated.

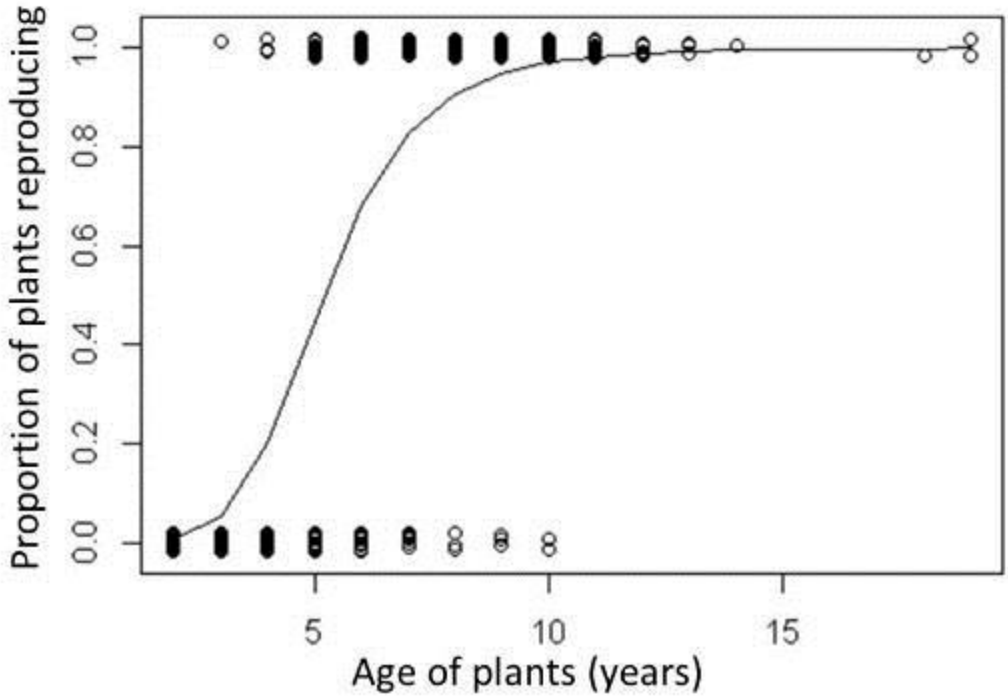

Fig. 2.3. Age at onset of reproduction for *Melaleuca parvistaminea*, indicating that 40% of plants were reproducing by the age of five. The curved line is from a fitted generalized linear model with binomial errors and log (age) as explanatory variable (n=617).

2.3.3 Bioclimatic suitability and invasive risk assessment

The areas predicted to be climatically suitable fitted well with the *M. parvistaminea* native distribution in Australia (AUC = 0.998, S2.4). Although the southern parts of Western Cape Province (Fig. 2a) are climatically very similar to the natural range of *M. parvistaminea*, the Tulbagh-Wolseley area where the only known invasive populations of the species occur at present is not climatically similar. Precipitation seasonality (33%) was the best contributor to the model, followed by isothermality (mean diurnal range/temperature annual range) contributing 31.2%.

In terms of an invasive risk assessment, 41 of the 47 questions relevant to *M. parvistaminea* were answered, leading to a score of 9 which would have resulted in the species being rejected in a pre-border evaluation (S2.6). According to the assessment, both agriculture and environmental sectors are at risk from invasion by this species. This species can clearly form dense monocultures (Fig. 2.1G) and overtop native vegetation (Breede Shale Renosterveld); its impacts are therefore likely to be similar to other invasive shrubs in the region that form impenetrable stands (reviewed by Richardson and van Wilgen, 2004). Wetter areas are preferred and dense stands form in seasonally waterlogged wetlands, posing a considerable threat if allowed to establish in large numbers after fire (Fig. 2.1E, H).

2.3.4 Post-clearing efficacy and post-fire recruitment

A follow-up survey indicated that cut material was not always stacked in the allocated dry areas. Seedling recruitment where cut adult plants had released seeds was observed in these areas. Fifty-two plants (mean height 172.9 cm, 158.4-187.4, 95% CI) were missed (3% of plants in the contract area); highlighting the role that monitoring and evaluation will have to play if eradication is to be achieved. Seedling recruitment at the allocated dead material stacks was restricted to shaded areas beneath the dead material. Searching should therefore focus on shaded areas in the vegetation and seedling establishment could be reduced by treating these shaded areas with herbicide. We observed no coppicing after cut stumps were treated with herbicide during April and May 2012. At the Waterval site, profuse germination (up to 18 000 seedlings/m^2, mean 4700 seedlings/m^2, 2600-6700 95% CI, n=29) was recorded within the canopy area of the burned adult plants, although low numbers were recorded up to 50 m away from adults. We observed that adult skeletons shade seedlings thereby improving likelihood of survival.

No herbicide was applied to 419 plants that had been cut at 23 (± 12) cm high (as a result of indiscriminate brush cutting as part of routine management block maintenance). These plants coppiced. We also observed several large plants (stem diameter greater than 5 cm) that had been cut less than 10 cm from the ground. There was no indication that herbicide had been applied (a coloured paint is routinely administered with herbicides), but these plants showed no signs of regrowth. This suggests that clearing efficacy is dependent on the height of the cut as well as herbicide application to cut stumps. Cut material was not removed from the area and was often found adjacent to resprouting plants. Profuse recruitment was sometimes seen near cut plants, i.e. large numbers of young plants of a similar age were observed.

2.3.5 Cost for eradication and management strategy

Our surveys indicated that *M. parvistaminea* is confined to the area between the Waterval Mountains and unsuitable cultivated/urban land of the Breede River Valley (Fig. 2.4). Fig. 2.4 indicates suitable areas (characterised by Breede Shale Renosterveld associated with forestry management) where *M. parvistaminea* could occur; this area will be the focus of future “search and destroy” contracts. To verify that the species had not spread along likely streams, we surveyed ~ 5km downstream of the Kluitjieskraal wetland and Waterval and found no plants.

Remaining areas at the three sites need to be surveyed. Based on the costs of surveying (without clearing), we estimate that a further ZAR 300 000 is required to survey (without clearing) the remaining 1 852 ha in 2014. Assuming that the remaining area at the Waterval, Kluitjieskraal plantation and wetland sites have invasive populations of similar density and that no new populations are found during the delimitation surveys, ZAR 427 000 is needed to clear all plants. Initial clearing should be completed by the end of 2014. A main aim of management is to prevent seed production, and eradication can only be declared once all current seedlings are detected and controlled before they set seed. Since >90% of the plants will flower at 7 years (Fig. 2.3), we estimate that eradication could be declared if no mature seed-capsules are observed on plants for seven years and there are at least two full surveys conducted that did not find any plants. Again assuming that all areas are invaded, follow-up surveys with clearing of seedlings and juvenile plants in the entire area will cost ZAR 496 000 each. Plants smaller than 0.8 m in height (and younger than 4 years) are unlikely to flower and due to similarity of native ericoid shrub species to these juveniles, low levels of detectability are expected for these plants. We therefore recommend that search and destroy operations should take place annually to prevent seed set in any missed plants. Thus we estimate that annual search and destroy operations for the next 7 years will cost ZAR 3 475 000 and eradication could be declared in 2021 at the earliest. Results regarding the *M. parvistaminea* invasion have been consolidated in S5.

2.4 Discussion

While eradication of invasive plants occurring over areas greater than 1000 ha has been shown to be difficult to achieve in the past (Rejmánek and Pitcairn, 2002), several features of this invasion both in terms of the biology of the plant and the management context suggest that eradication of *M. parvistaminea* (invasion ~ 1800 ha) could be achieved in South Africa. However, monospecific stands are likely to over-top native vegetation, the species has the traits of a transformer species (excessive user of resources and a fire promoter, sensu Richardson et al. (2000)) and so the invasion will likely have a large impact if given time and allowed to spread to suitable habitats. Therefore *M. parvistaminea* is an appropriate target for eradication.

2.4.1 Origin of the invasion

At the Waterval site evidence of large decaying adult trees were observed. This observation and age-ring data taken during the study suggest that the species was introduced before 1990 (~10 years prior to when the oldest plants established). Although Richardson and Rejmánek (2011) recorded this species (listed as *M. ericifolia*) as an ornamental plant, we could find no evidence of this species being introduced or sold for this purpose in South Africa (Poynton, 2009) and neither were any planted trees recorded. We suspect that the plants were introduced to the Kluitjieskraal nursery (van Wyk et al., 2012), and that seeds dispersed from there in soil used for planting of pine seedlings.

2.4.2 Local delimitation and population dynamics

Failed eradication attempts are commonly characterised by lack of population delimitation (Panetta and Lawes, 2005; Panetta et al., 2011). We recommend therefore that the unconfirmed report at Suurvlak plantation be resurveyed by systematic searching when plants are likely to be more detectable and assuming all adult plants were destroyed in the fire of January 2012, this should be done in 2014 to coincide with first flowering. The absence of established plants along tributaries of the Berg and Breede rivers supports our case for eradication of the species.

From initial surveys and the lack of other records, we conclude that naturalised populations of *M. parvistaminea* are currently restricted to the Tulbagh-Wolseley area. In this one area there are now several clear foci of invasions across a spectrum of land-uses types with a distribution large enough that it should be classified as fully invasive, i.e. category E under the Blackburn et al. (2011) scheme. Spread is only through seeds which require water for germination (Robinson, 2007) and is encouraged by fire and clearing which triggers seed release. Seeds remain viable for one year (Robinson, 2007), suggesting that a long-lived soil seed bank is absent. This favours a much shorter time for eradication than for some of the Australian acacias (Wilson et al., 2011).

2.4.3 Management recommendations

Implementing an eradication plan for the first known invasion by this species anywhere in the world would have substantial significance from a management perspective, but much of the work still needs to be done.

Areas which are particularly at risk in South Africa are those with similar land use and habitat requirements. Places where Breede Shale renosterveld is associated with plantation or forestry exit areas are likely candidates for further surveying. The bioclimatic model however indicates that the Tulbagh-Wolseley area is not ideal for *M. parvistaminea*. Of concern is the fact that the southern Cape (Fig. 2.2a) is highly suitable for this species. These areas will form the basis for continued regional and national scale surveys for *M. parvistaminea*.

No prior intentional management of the species has taken place at any of the sites that were surveyed. Clearing of *M. parvistaminea* (among several other native and alien species) as the unintended part of routine maintenance of pine-planted blocks has been largely ineffective (due to a lack of herbicide application and cutting too high from the ground) and likely triggered seed release contributing to spread. Plants at the Kluitjieskraal wetland were probably missed because they were not flowering at the time of clearing (April-May 2012). GPS tracks were not taken during the clearing operations and the effectiveness of the management could therefore not be verified. Systematic survey methods need to be followed if eradication is to be achieved and documented. To prevent spread from the area, no material should be removed. Seedling recruitment in wet areas can be avoided by stacking dead material in dry areas, sites that should be the focus for follow up control. Herbicide (triclopyrtriethylammonium salt–Lumberjack™) applied to cut stumps as per Working for Water standard protocol, has been very effective, with no evidence of resprouting after treatment. No treatment of seedlings has yet been undertaken, but potentially a foliar spray could be used on juvenile plants after three years (reproductive onset is at five years) when densities of seedlings have declined and plants are bigger and therefore more visible. Identification of non-reproducing plants could be difficult as *M. parvistaminea* is easily confused with ericoid fynbos species (e.g. *Passerina* species). The aromatic, eucalypt-like smell of the leaves is however unmistakeable and a valuable quick and easy field identification tool.

We further suggest, that as part of management operations, the position of every plant, height (as the best predictor of age) and presence/absence of reproductive structures be measured to inform the adaptive management framework. The area searched should be recorded (using track logs), so that the completeness of survey can be confirmed. Standard control operations are likely insufficient to eradicate the species, so some additional intensive follow-up monitoring, to see if plants have been missed and determine effectiveness of control should be done (Zenni et al., 2009).

2.4.4 Eradication feasibility

Several factors suggest that the eradication of *M. parvistaminea* is a realistic goal (Simberloff, 2003; 2009; Panetta and Timmons, 2004; Panetta et al., 2011). Serotinous species generally do not have seed dormancy adaptations and are relatively short-lived in the soil seed bank (Robinson 2007). Our observations support this notion for *M. parvistaminea*, given that Robinson (2007) reported a seed viability of one year for the species. We therefore do not expect any germination from the seed bank after the fire at the Waterval site in January 2012. The absence of a soil-stored seed bank is arguably what minimizes the risk this species poses the most. When compared to species that store seeds in soil, not only does this reduce control costs, but also means that fewer clearing follow ups are required to declare areas as completely cleared. Fire could be a useful tool to kill adult plants and initiate a once off seed release event. In the absence of fire or clearing, *M. parvistaminea* can however release seeds intermittently through the death of stems (Robinson, 2007).

Lack of sufficient resources (including post-eradication surveys and follow-up) has been put forward as a reason for failed eradication projects (Simberloff, 2009). Ensuring that enough money is available from start to the end is thus vital to the success of an eradication project. As a core part of the mandate of the Invasive Species Programme at the South African National Biodiversity Institute (SANBI's ISP), there is a national organisation responsible for ensuring that the necessary resources are available until eradication is declared (Wilson et al., 2013). This study forms the basis for the eradication plan for this species, which SANBI's ISP will implement.

Although a formal cost-benefit analysis was not conducted in this study, we strongly believe that the substantial reduction of *M. parvistaminea* populations by 2014 (after initial clearing) will ensure that impacts are minimised. Benefits of eradication are assumed to be a reduction in the national invasion debt (Wilson et al., 2013) and conservation of native biodiversity with its associated benefits. Costs of follow up surveys and clearing will also be considerably less, suggesting a favourable cost-benefit ratio. Since forestry and nursery trials no longer take place at Kluitjieskraal forestry station (Poynton 2009), we do not anticipate further reintroductions of the species via this pathway.

The eradication cost of ZAR 3 345 000 is uncertain, but with continued survey data and contextual info, estimates will be revised. Additional localities might be found, while if extra follow ups are deemed necessary (also if management effectiveness is low), the eradication cost is likely to increase. These uncertainties are why van Wyk et al. (2012) suggest that operating in an adaptive management framework where estimates of risk, cost and time are continually revised as contexts shift and information can be used to update the risk profile. This is only possible if data on the progress of management are collected and interrogated (e.g. on an annual basis). In comparison with costs estimated for a similar size and eradication time for species in Australia (Panetta et al., 2011), the costs estimated in this study are an order of magnitude less.

In conclusion we recommend that an eradication plan is implemented against *M. parvistaminea* and the species is listed under category 1a of the invasive species regulations of NEM:BA (Department of Environmental Affairs, 2014), i.e. requiring compulsory control. Given the invasive potential of this species and uncertainty around taxonomy of introduced species in the group we further suggest the need for a comprehensive assessment of invasive dry-fruited Myrtaceae in South Africa.

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Chapter 3: Recent discovery of small naturalised populations of *Melaleuca quinquenervia* in South Africa

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Author contributions:

LEOJ, EvW, JRUW planned the study

LEOJ: Collect the data, undertook the risk assessment, and wrote the first draft of the paper

EvW: Sourced the bioclimatic model, and edited the manuscript

JRUW: Provided overall guidance and edited the manuscript

Abstract

The discovery of a naturalised population of *Melaleuca quinquenervia* in South Africa in 2009 prompted an evaluation of the species' distribution across South Africa. We found records at seven localities in two of the nine provinces of South Africa, with naturalised populations at two sites—~300 plants were discovered over 0.3ha in a confined-seep on a mountain slope, while at an old arboretum 12 large, planted trees and 9 naturalised trees were found. An additional herbarium record from Mozambique suggests that this global invader is present at other sites within the sub-region, and so while the extirpation of populations in South Africa is recommended and looks feasible, further work is required to determine the status and evaluate whether eradication from the sub-region as a whole is possible.

Keywords: early detection, eradication, Myrtaceae, tree invasions

3.1 Introduction

The publishing of new records for naturalised and potentially invasive tree species is important for a number of reasons (Wilson et al., 2014a). It helps informs risk assessment and allows for appropriate response planning and for rapid information dissemination (Lucy and Panov, 2012). This helps in the compilation of lists of invasive species which are widely used by scientists, managers and policy makers. These lists can, however, be prone to a range of errors (McGeoch et al., 2012), highlighting the importance of publishing accurate records for introduced species.

Melaleuca quinquenervia (Cav.) S.T. Blake, the broad-leaved paper-bark, is a tree (up to 25 m tall) native to eastern Queensland and New South Wales in Australia, and to parts of Indonesia, New Caledonia and Papua New Guinea (Blake, 1968; Serbesoff-King, 2003). In its native range, it typically occurs in coastal wetlands that are temporarily inundated, along freshwater stream banks and in brackish water adjacent to mangrove swamps (Turner et al., 1998).

The species has been widely disseminated throughout the world mostly as an ornamental species, but occasionally to aid with draining wetlands (in particular in the United States of America). It is known as invasive in the Americas and on islands in the Pacific and Caribbean, but has not previously been recorded as naturalised in Africa (Rejmánek and Richardson, 2013) (definitions for naturalised and invasion are as per Blackburn et al., 2011). It is most notorious as a transformer species (sensu Richardson et al., 2000) of the Florida Everglades of the United States, where, by 1998, it had invaded an estimated 202 000 ha (Turner et al., 1998; Dray et al., 2006; Martin et al., 2009; TAME, 2014). Plants form extensive monocultures that exclude native vegetation and provide large fuel loads for fires, leading to substantial ecosystem level impacts. Between 1989 and 1999 the US government spent US$ 25million on controlling the species (Serbesoff-King, 2003).

In May 2009, a small population of *M. quinquenervia* was found by a field ranger in a moist seep in the mountains near the town of Wolseley in the Western Cape Province of South Africa. Given the species' history of invasiveness elsewhere, it was deemed to be of high risk and was prioritized for further evaluation and management (van Wyk et al., 2011). Here we document the localities and their invasion stage in South Africa (and southern Africa more broadly), explore possible introduction histories and conduct a qualitative assessment of risk.

3.2 Methods

3.2.1 Determining current distribution in South Africa

Publicity leaflets were developed and 1000 were distributed (S3.1) as part of a country-wide survey strategy. We targeted land managers (mainly conservation and forestry) and invasive plant researchers (at national workshops and conferences) as a basis for knowledge of where these plants may be. In addition to these publicity efforts, we searched for records of the species in herbaria (Table 1), with specimens confirmed as *M. quinquenervia* by the *Melaleuca* taxonomic authority in Australia (B. Lepschi, pers. comm.). Table 3.1 lists the records that we found and indicates the invasive status of each instance. In a national survey of tree collections, respondents have been asked to specifically submit historical and current records of *Melaleuca* plantings (including *M. quinquenervia, M. styphelioides* and *M. parvistaminea*). To determine and understand the introduction history of *M. quinquenervia* at each site, we reviewed historical records and interviewed relevant land managers.

At Wolseley we conducted systematic surveys of the area in 2009 and in 2012 to determine the extent of the population. This was done by walking parallel transects using a handheld GPS (Fig. 3.2) and recording any plants that were found. At Tokai, we searched for recruitment in an area around the planted trees (Fig. 3.4). To further delimit the extent of the two naturalised populations, we investigated likely dispersal pathways, i.e. along watercourses.

3.2.2 Invasive potential and risk assessment

To assess the potential invasiveness of the species in the region, different bioclimatic models were developed using BIOMOD (Thuiller, 2003). All BIOCLIM variables (www.worldclim.org/bioclim) were used with an aspect of 2.5 arc minutes resolution (4.6 km x 4.6 km). Native range localities were selected from Australia's Virtual Herbarium (avh.ala.org.au/), and the Global Biodiversity Information Forum (www.gbif.org). For projection onto South Africa, both naturalised (Table 1) and native range localities were used.

To collate species information, determine invasive potential and identify areas requiring more research, the Australian Weed Risk Assessment (WRA) (Pheloung et al., 1999) was used. This WRA has been applied widely and is reported to be consistently accurate (Gordon et al., 2008, 2010; Hulme, 2012). It also provides a standard method for collating information on potential impacts.

Table 3.1

Records of *Melaleuca quinquenervia* from southern Africa (also see Fig. 3.1), with invasion status as per Blackburn et al. (2011). None of the populations can be definitively classed as fully invasive (E under the Blackburn scheme). While the source of both the Wolseley and Krantzkloof plants is not known, at neither population has dispersal to and reproduction at multiple sites been recorded.

Site	Population size	Status	Landscape context	Herbarium specimens
Durban Botanical Gardens, Kwa-Zulu Natal S29.84585 E31.00601	One tree	B2, planted	Botanical gardens in an urban setting	NH-72446 (BJ Pienaar 345),
Krantzkloof Nature Reserve, Kwa-Zulu Natal S29.76243 E30.85594	Unclear, one plant found on resurvey	Probably D1–E, not planted, presumed naturalised	Nature reserve in a valley surrounded by urban areas	M. Cheek 946
Paarl Arboretum, Western Cape S33.85710 E18.49742	2 large adult trees	B2, planted	Arboreta in an urban setting, but with opportunities for recruitment	none
Tokai Arboretum, Western Cape S34.05745 E18.42323	12 mature very large individuals in rows (> 73 cm stem diameter); 9 juveniles (3-4 m high) recruited, flowering and producing seeds	C2 or C3, naturalised	Picnic site adjacent to the oldest arboretum in South Africa	NBG-269274 (M Tywalana 64)
Wolseley, Western Cape S33.43422 E19.14405	~300 mature individuals over 0.28 ha	C3 or D2, source unknown, naturalised	Previously commercial forestry land, 570 meters above sea level	NBG-0262932 (E van Wyk 2)

Site	Population size	Status	Landscape context	Herbarium specimens
Durban, KwaZulu-Natal, no specific locality given	Unknown	Unknown	Urban setting (uncertain)	NH-41052
Durban, KwaZulu-Natal, Pine Town, Bamboo Lane S29.8206 E30.8692	Unclear, presumed to be 1 plant in 1982. Survey required	B2 or B3, presumed planted	Urban setting	NH-75265 (AM Rowe s.n.), NH-39297
Ponta Barra Falsa/Pomene, Mozambique Coordinates undetermined	Unclear, adults and seedlings present. Survey required	C3 at least, potentially E	In and around a wetland	PRE-855502

3.3 Results

3.3.1 Determining the current distribution in South Africa

Of the eight records we found, naturalised populations occur at Tokai and Wolseley in the fynbos region of the Western Cape, Krantzkloof (Durban) in the subtropical KwaZulu-Natal province of South Africa and in the tropical Mozambique (Table 3.1). The herbarium specimen collected in Mozambique stated that the species was naturalised. No records were reported through leaflet (S3.1) distribution.

The naturalised populations at Tokai (Fig. 3.4, 3.5) and Wolseley (Fig. 3.2, 3.3) were not very extensive, 21 and ~ 300 plants respectively (Table 1). At Krantzkloof, apparently the reserve managers had identified *M. quinquenervia* as being problematic in the early 2000s and over three field seasons had made a concerted effort to eradicate it from the area (J. Vermeulen, pers. comm.). A complete survey of the area is still required to assess the success of the control operations and the possible introduction routes by which the plant arrived in the area.

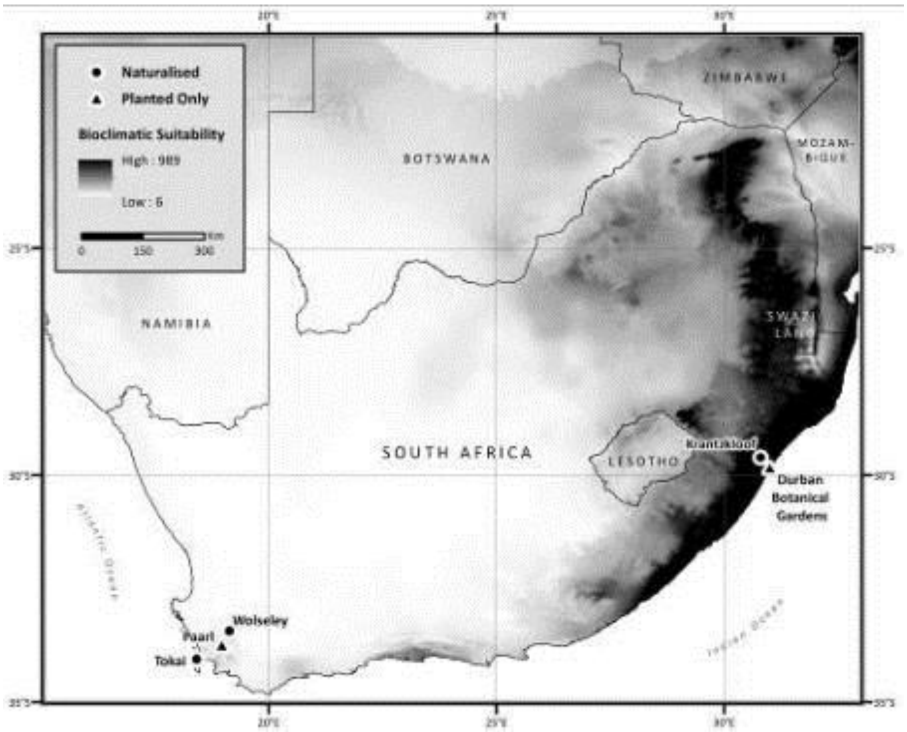

Fig. 3.1. Known records of *Melaleuca quinquenervia* in South Africa indicating planted or naturalised status at each location. The predicted climatically suitable range of the mean consensus of models run in BIOMOD is indicated by the shading (darker areas are more suitable).

3.3.2 Invasive potential and risk assessment

The models gave qualitatively similar results in line with other distribution models for this species (e.g. Watt et al., 2009), with sensitivity and specificity higher than 98% (Fig. 3.1; S3.2). Although the known localities of *M. quinquenervia* in the southern Western Cape were included in the models, this region was not predicted to be highly suitable. Instead, the sub-tropical east coast and savanna ecosystems in South Africa are most at risk of invasion (Fig. 3.1).

We derived a score of 21 from the Australian WRA (S3.4), indicating the considerable risk the species poses in South Africa. Among the undesirable traits as an invader (identified in the WRA) is the ability of *M. quinquenervia* to form dense thickets, increase fire hazard, prolific seed production and persistent canopy seed bank. A synopsis of *M. quinquenervia* at this invasion stage (naturalised) in South Africa is given in S3.3.

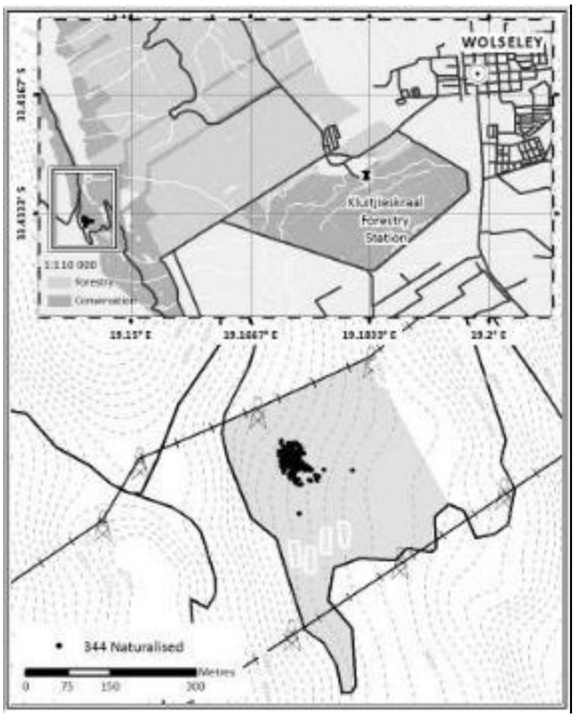

Fig. 3.2. Distribution of the largest known population of *Melaleuca quinquenervia* at Wolseley, Western Cape. Grey shading indicates the area that was surveyed.

3.4 Discussion

Melaleuca quinquenervia is naturalised at four sites in southern Africa, but is likely present at several sites, posing an invasion threat considering the species' invasiveness elsewhere (Rejmánek and Richardson, 2013). Indications from bioclimatic modelling and risk assessment (21 for *M. quinquenervia* compared to 9 for *M. parvistaminea* and 18 for *Acacia paradoxa* (Zenni et al., 2009) further support this invasive threat status in the sub-region. Thus far however, the species appears to have only been introduced at a limited number of sites. With several World Heritage Sites and Wetlands of International Importance (Ramsar sites) in the region (iSimangaliso Wetland Park, parts of the Cape Floristic Region, Okavango Delta), this species should be put on watch lists across the region, and all historical plantings and naturalised populations removed. The bioclimatic modelling did not, however, predict that the Tokai or the Wolseley sites where naturalisation occurred were climatically suitable. We suspect that this might be because the species is more limited by micro-site conditions for germination than broad-scale climate, but equally this might explain its low rate of spread at both sites. Further work is required on this, but without a strong mechanistic explanation for why the CFR is not suitable, we would recommend a precautionary approach and that the species should be intensively managed wherever it is found in the region.

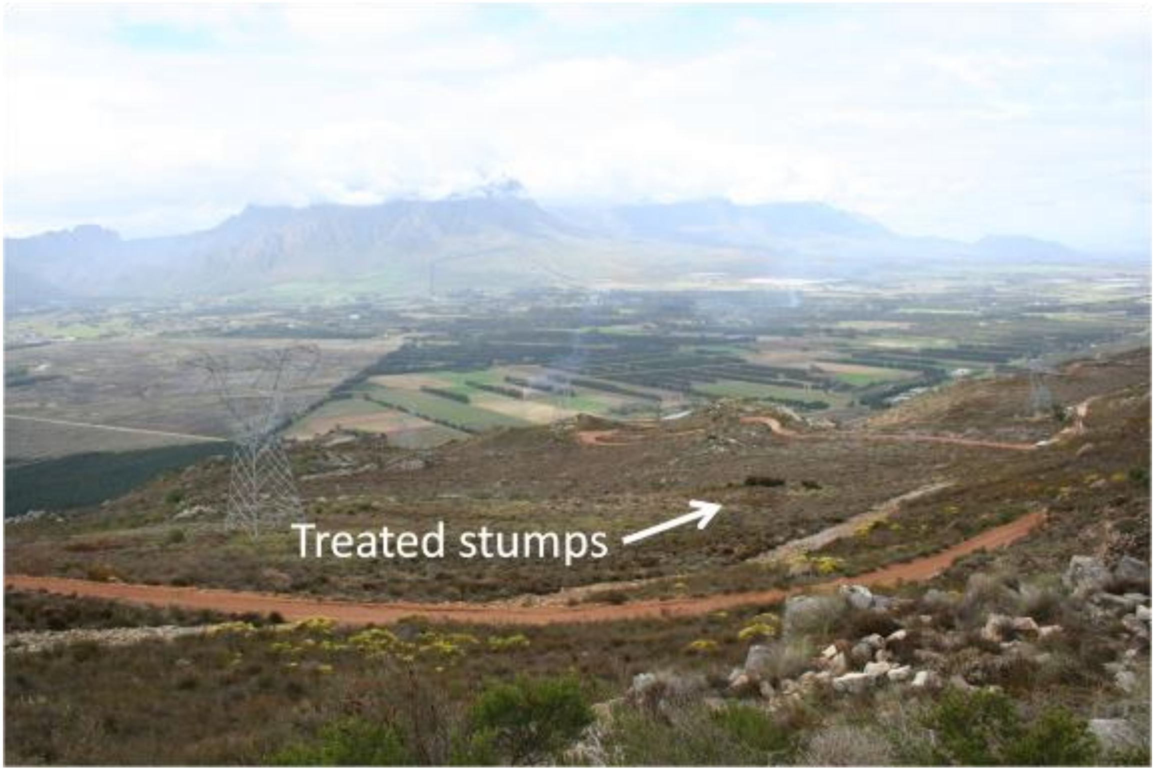

Fig. 3.3. Contextual landscape setting indicating the situation of the treated stumps of the *Melaleuca quinquenervia* population on a fynbos mountain slope above Wolseley in the Breede River valley. The main land uses in the valley are for agriculture and silviculture.

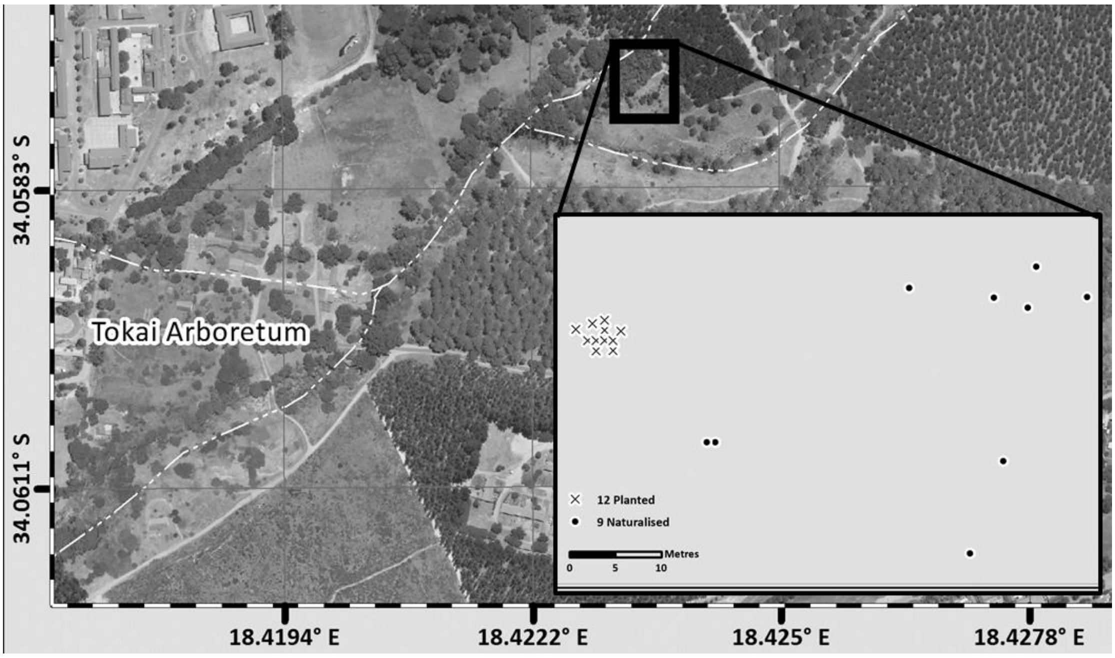

Fig. 3.4. The naturalised population at the Tokai plantation in Cape Town, Western Cape, indicating proximity to the arboretum and surveyed area in grey (inset).

Fig. 3.5. The planted (P) and naturalised (N) *Melaleuca quinquenervia* plants at the Tokai plantation, Cape Town, Western Cape.

There are various elements which contribute to the success and failure of eradication projects (e.g. Mack and Lonsdale, 2002; Simberloff, 2009). Of these, several factors bode well for the eradication of the species from South Africa: (1) naturalised populations are apparently extremely localised and small; (2) plants require a wet soil surface or dry-wet cycles to germinate so are restricted to specific habitat types (Rayamajhi et al., 2002; Van et al., 2005); (3) seed viability in the soil is usually less than two to three years (Rayamajhi et al., 2002; Van et al., 2005); (4) flowering *M. quinquenervia* plants (i.e. before seed-set) are highly visible in the matrix of native vegetation thereby facilitating detection; and (5) current institutional arrangements are in place to ensure diligent attention to monitoring and treatment. This study supports the prioritization of this species by the South African National Biodiversity Institute's Invasive Species Programme for eradication from South Africa (Wilson et al., 2013), and suggests the species should be listed as an eradication target (i.e. category 1a) under South African invasive species regulations (Department of Environmental Affairs, 2014). Dawson et al. (2008) identify the role botanical gardens play at various stages of invasion. Thus given the landscape context of the naturalised and planted records, (Table 3.1) we suggest that arboreta, botanical gardens and forestry stations should provide some focus for future search efforts.

A major issue that remains to be resolved is how the naturalised plants got to their current locations. The Wolseley population is on land previously managed by the Kluitjieskraal Forest Station, established in 1884 (King, 1938; J. Storr-Lister, undated Compilation of Annual Reports). Although *M. quinquenervia* is not mentioned, nursery import records for Kluitjieskraal from the late 1800s show that *Melaleuca parvistaminea* Byrnes and *Melaleuca styphelioides* Sm. were imported and planted as potential hedges and wind-breaks. While both *M. parvistaminea* and *M. styphelioides* have since become invasive in the wetlands adjacent to the nursery at Kluitjieskraal, no *M. quinquenervia* have been found in this area (Jacobs et al., 2014; van Wyk et al., 2011). The naturalised population of *M. quinquenervia* is some 3.5km from the nursery site on a slope 300m above the valley floor. The nearest confirmed extant *M. quinquenervia* plants are in Paarl Arboretum about 40km away (Fig. 3.1) over a range of mountains. As the site is next to power-lines and a road (Fig. 3.2; 3.3), the population may have originated from seed brought to the site accidentally with equipment during the construction of these facilities or during maintenance or harvesting of commercial forest plantations in the area. The Krantzkloof Nature Reserve is in an urban context and the population could have come from neighbouring gardens (reserve surrounded by properties with extensive gardens). There are anecdotal records of historical plantings close by, but more needs to be done to ascertain the source. The only other extant individuals are at Durban Botanic Gardens >20 km away and several hundred metres lower in altitude.

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Chapter 4: Quantifying errors and omissions in alien species lists: The invasive status of *Melaleuca* species in South Africa as a case study

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Author contributions:

LEOJ, JRW, DMR: planned the study

LEOJ: Collected data, identified specimens, undertook analysis, made maps and wrote the first draft of the paper

BJL: Confirmed identifications and provide assistance and guidance around *Melaleuca* taxonomy

LEOJ, JRW, DMR, BJL: edited and commented on the manuscript

JRUW: provided overall guidance

Abstract

Introduced species lists provide essential background information for biological invasions research and management. The compilation of these lists is, however, prone to a variety of errors. We highlight the frequency and consequences of such errors using introduced *Melaleuca* (sensu lato, including *Callistemon*) species in South Africa as a case study. We examined 111 herbarium specimens from South Africa and noted the classes and types of errors that occurred in identification. We also used information from herbarium specimens and distribution data collected in the field to determine whether a species was introduced, naturalized and invasive. We found that 72% of the specimens were not named correctly. These were due to human error (70%) (misidentification, and improved identifications) and species identification problems (30%) (synonyms arising from inclusion of *Callistemon*, unresolved taxonomy). At least 36 *Melaleuca* species have been introduced to South Africa, and field observations indicate that ten of these have naturalized, including five that are invasive. While most of the errors likely have negligible impact on management, we highlight one case where incorrect identification lead to an inappropriate management approach and some instances of errors in published lists. Invasive species lists need to be carefully reviewed to minimise errors, and herbarium specimens supported by DNA identification are required where identification using morphological features is particularly challenging.

Keywords: Biological invasions, *Callistemon*, herbarium specimen, invasive species listing, Myrtaceae, tree invasions

4.1 Introduction

Species lists form the basis for much of the current research on biological invasions (e.g. the Global Naturalized Alien Flora Database of van Kleunen et al., 2015). Such lists are also essential for guiding legislation, as input to decision making and risk assessment, and in the formulation of management policies and strategies (McGeoch et al., 2012; Latombe et al., 2016). Because resources required to address the threat of invasive species are limited, objective categorization of species is required to prioritize resource allocation according to species, areas and introduction pathways (McNeely et al., 2001, Nel et al., 2003; Wilson et al., 2013). Accurate lists of alien species, with data on their introduction status, are thus crucial resources, not just for the regions for which they are compiled, but also globally (Wilson et al., 2011). But, as with any information derived from a variety of sources, the compilation of lists is prone to a number of errors which can then be perpetuated in various ways (McGeoch et al., 2012). To address these concerns, it is thus essential that the error rates in species lists are assessed and ways to detect them are identified.

Pyšek et al. (2002) include alien taxa and their status in a flora of the Czech Republic. This well-compiled list lends itself to comparison with other regions and is an important example allowing for determinants and patterns of plant invasions at a global scale to be studied (Pyšek et al., 2004). Such lists are the essential building blocks on which assessments of the status of invasions in a country should be built (Latombe et al., 2016). By comparison, even though South Africa has a reasonably well-funded national programme for controlling invasive species, especially plants, research on lesser known invasive groups has only recently been given special attention (Wilson et al., 2013), and there is no comprehensive list of introduced and invasive species (Faulkner et al., 2015). A list of regulated invasive plant species was published in 2014 and this forms the basis for management plans and regulation (Department of Environmental Affairs, 2014). However, this regulatory list is incomplete and contains omission and synonym errors (per. obs.). Moreover, more species will need to be added as surveillance progresses, as more species demonstrate invasiveness, impacts are evaluated, and as errors in the list are discovered (Rouget et al., 2016).

For plants, herbaria are indispensable resources and reference sources for much botanical research which requires reliable species identifications, including the compilation of introduced species lists (Glen, 2002). Funding for taxonomy and the upkeep of herbaria is declining worldwide (Smith et al., 2008; Guerin, 2013; Pyšek et al., 2013) and is a concern that can be compounded because expertise for alien species is less likely to exist in any particular country. Herbarium specimens, upon which comprehensive lists are ideally based (Pyšek et al., 2013), require curation as taxa are revised or new information becomes available, e.g. from molecular and other studies (e.g. Le Roux et al., 2010). Many alien taxa are underrepresented, remain unidentified for considerable periods of time, or are misidentified in herbaria (Pyšek et al., 2013). In this paper we explore the scale of this problem using taxa in the genus *Melaleuca* (sensu Craven (2006) and Brophy et al. (2013)) in South Africa as a case study.

The genus *Melaleuca* has not been distributed around the world as extensively as some other tree groups (e.g. *Eucalyptus,* a sister genus in the Myrtaceae) (Rejmánek and Richardson, 2011). However, seven species are listed as invasive in the USA and South Africa (Rejmánek and Richardson, 2013), including one of the world's poster-child plant invaders, *Melaleuca quinquenervia,* which has invaded large areas and caused major damage in the Everglades region in Florida (Richardson and Rejmánek, 2011). The genus has about 290 species consisting of shrubs and trees, a number of which are planted in many parts of the world, largely as ornamentals, but also for timber, honey, bark and plant extracts (Brophy et al., 2013). Widespread cultivation of *Melaleuca* species is relatively recent, especially when compared to other genera in the Myrtaceae such as *Eucalyptus*, and records of naturalization and invasions in South Africa (Jacobs et al., 2014, 2015) and other parts of the world (Rejmánek and Richardson, 2013) are comparably recent. Several species are recorded as weedy within Australia (Randall, 2007), perhaps indicating that these (mostly) fire-adapted species could pose a risk to areas with similar fire-prone areas, such as the Cape Floristic Region of South Africa which has been invaded by many other woody plants from Australia (Wilson et al., 2014b).

In 2009, the discovery of several naturalised populations of *Melaleuca* species in South Africa prompted an evaluation of the introduction status for the entire group in the country (Wilson et al., 2013). Taxa such as *Melaleuca armillaris* subsp. *armillaris*, *M. viminalis* subsp. *viminalis* and *M*. *citrina* have been widely planted in South Africa and also warranted further study. This also provided an opportunity to reassess the accuracy of current published lists.

Here, we compile a list of *Melaleuca* species recorded as present in South Africa and determine the invasive status of each species. We use herbarium specimens to do this, while also noting the extent to which they are accurately identified and the types of errors which occur. We discuss consequences of errors and omissions and make recommendations on how these could be avoided and addressed.

4.2 Methods

4.2.1 Taxonomy

Generic limits in the tribe Melaleuceae have been the subject of much recent study (Brown et al., 2001; Wilson et al., 2005; Craven, 2006; Edwards et al., 2010; Udovicic and Spencer, 2012; Craven et al., 2014). We follow Craven (2006), Edwards et al. (2010) and Brophy et al. (2013) in adopting a broad concept of *Melaleuca*, i.e. including *Callistemon*. The further expansion of the genus *Melaleuca* to include *Beaufortia*, *Calothamnus*, *Conothamnus*, *Eremaea*, *Lamarchea*, *Petraeomyrtus*, *Phymatocarpus* and *Regelia* (Craven et al., 2014), has not yet been fully evaluated by the Australian taxonomic community, and these taxa are excluded from consideration for this study. Many *Melaleuca* species (especially those formerly recognised as *Callistemon*) are morphologically similar which makes them difficult to identify using morphological features. Several cultivars have been developed for some *Melaleuca* species in the *Callistemon* group and difficulty in identifying such specimens in South Africa is perhaps due to horticultural selection and the existence of both sexual and apomictic species within the group (Craven, 2009; Brophy et al., 2013).

4.2.2 Review of herbarium specimens and error classification

Herbarium specimens from the Compton herbarium (NBG) were examined to check whether specimen identifications were correct, and to provide accurate identifications where necessary. To do this, we used the taxonomic literature to compare morphological characters on the specimens with descriptions and taxonomic keys (in particular Craven and Lepschi, 1999 and Brophy et al., 2013). Photographs and high-resolution scans of the specimens were taken for verification and future reference. Specimen identifications were checked against referenced herbarium specimens housed at the Australian National Herbarium (CANB; herbarium codes follow Thiers, 2016). The identifications of all specimens were subsequently confirmed by a taxonomic authority for *Melaleuca* (B.J. Lepschi).

Herbarium specimens were examined in 2013; any specimens accessioned or re-identified after this date were not included in the analysis. McGeoch et al. (2012) proposed an uncertainty classification that separates epistemic and linguistic errors into ten sub-categories. In this study we focussed on two of these sub-categories—human error and species identification. In keeping with terminology from McGeoch et al. (2012), we define the word "error" to be inclusive of actual and potential errors. For example, although a species name on a specimen was not currently accepted but no obvious mistake in listing arose from this yet, it was still recorded. As per McGeoch et al. (2012) scheme the human errors we discovered in this study were: misidentifications, and improved resolution of the identification (e.g. *Melaleuca* sp. identified as *M. parvistaminea,* or *M. armillaris* as *M. armillaris* subsp. *armillaris*). The only species identification error was unresolved taxonomy. A description of the different errors and how they were determined is shown in Table 4.1, as well as the frequency and relative proportions of the errors. Because the inclusion of *Callistemon* in an expanded *Melaleuca* is still under debate, synonyms where the genus name *Callistemon* changed to *Melaleuca* were placed under the species identification error type (instead of human error as per McGeoch et al., 2012 treatment). No synonyms outside of this situation were found and therefore synonyms relating to human error were absent from our dataset. We also looked to see if there were any historical trends in the errors by comparing the years at which taxa with particular errors were collected to the years in which taxa with no error were collected using Mann-Whitney U tests in R.

4.2.3 List compilation

Once correct identification for all specimens had been confirmed, we used these specimens as the source for compiling a list of species present in South Africa. We also used a list of cultivated plants based on herbarium records in southern Africa (Glen, 2002), and a list of forestry trees and their uses in South Africa (Poynton, 2009). The minimum residence time in South Africa was determined from the date on the oldest herbarium specimen for each species.

Naturalized populations were reported by a variety of conservation agencies, with the reports collated by the South African National Biodiversity Institute's Invasive Species Programme and through the Southern African Plant Invaders Atlas (Henderson et al., 2007; Wilson et al., 2013).

We collected height data as an estimate of age, presence/absence of reproductive structures and GPS coordinates for each plant. Using these data we were able to determine whether a species is sustaining itself, whether it is reproducing and/or spreading, hereby indicating the status of each species as introduced, naturalized or invasive according to the subcategories proposed by Blackburn et al. (2011).

Table 4.1
Result of analysis of confirmed herbarium records (n=111), indicating the breakdown of correctly identified specimens with various error types. For full details see Supplementary Material (S4.1). The errors identified here are error type 1 (i.e. human error, indicated as HE) and type 3 (i.e. species identification indicated as SI) as per McGeoch et al. (2012); synonyms are included in type 3 here (see Methods (4.2)). The table only includes samples from the Compton Herbarium, Kirstenbosch (NBG).

Status	**Description**	**Number of herbarium specimens**	**Examples**
Correctly identified	The identification on the herbarium specimen was the same as determined by an expert in the group (the author: BL)	31	Seven specimens of *Melaleuca styphelioides* and five specimens of *M. hypericifolia* correctly identified
Misidentification (HE)	The identification on the herbarium specimen was to a currently accepted species, but not the correct one	31	*Melaleuca parvistaminea, M. armillaris* subsp*. armillaris and M. cuticularis* were misidentified as *M. ericifolia*,
Further identification (HE)	The identification on the herbarium specimen could be refined, either by providing the specific epithet or the subspecific epithet	25	Several specimens (e.g. *M. rugulosa*) only identified to genus level; *M. armillaris* could be identified further to subspecies level
Unresolved taxonomy (SI)	The taxonomy used to identify the herbarium specimen was not resolved at that time, so any name provided will have some uncertainty around it.	2	Several names misapplied to *Melaleuca quinquenervia* (prior to 1968)

Status	Description	Number of herbarium specimens	Examples
Synonym (SI)	The identification was confirmed, but the name on the herbarium specimen was not the most current accepted name	22	Nine specimens of *Callistemon rigidus* (a synonym of *C. linearis*, also a synonym of *Melaleuca linearis* var. *linearis*), *Callistemon viminalis* = *Melaleuca viminalis* subsp. *viminalis*

4.3 Results

4.3.1 Review of herbarium specimens

A summary of the errors found is in Table 4.1 with details of each specimen that required a name change in S4.1. Examples of the types of errors on are shown in Fig. 4.1. Of the 111 specimens examined, only 31 specimens carried a currently accepted name (excluding current names for specimens that were incorrectly identified). Misidentifications made up the largest proportion of errors, while poorly resolved taxonomy was the reason for two specimens being incorrectly named. All synonyms required at least the genus name to be changed. There was no significant effect of date of collection on whether an error was noted, or on particular error types (dates of collection varied between 1907 and 2013).

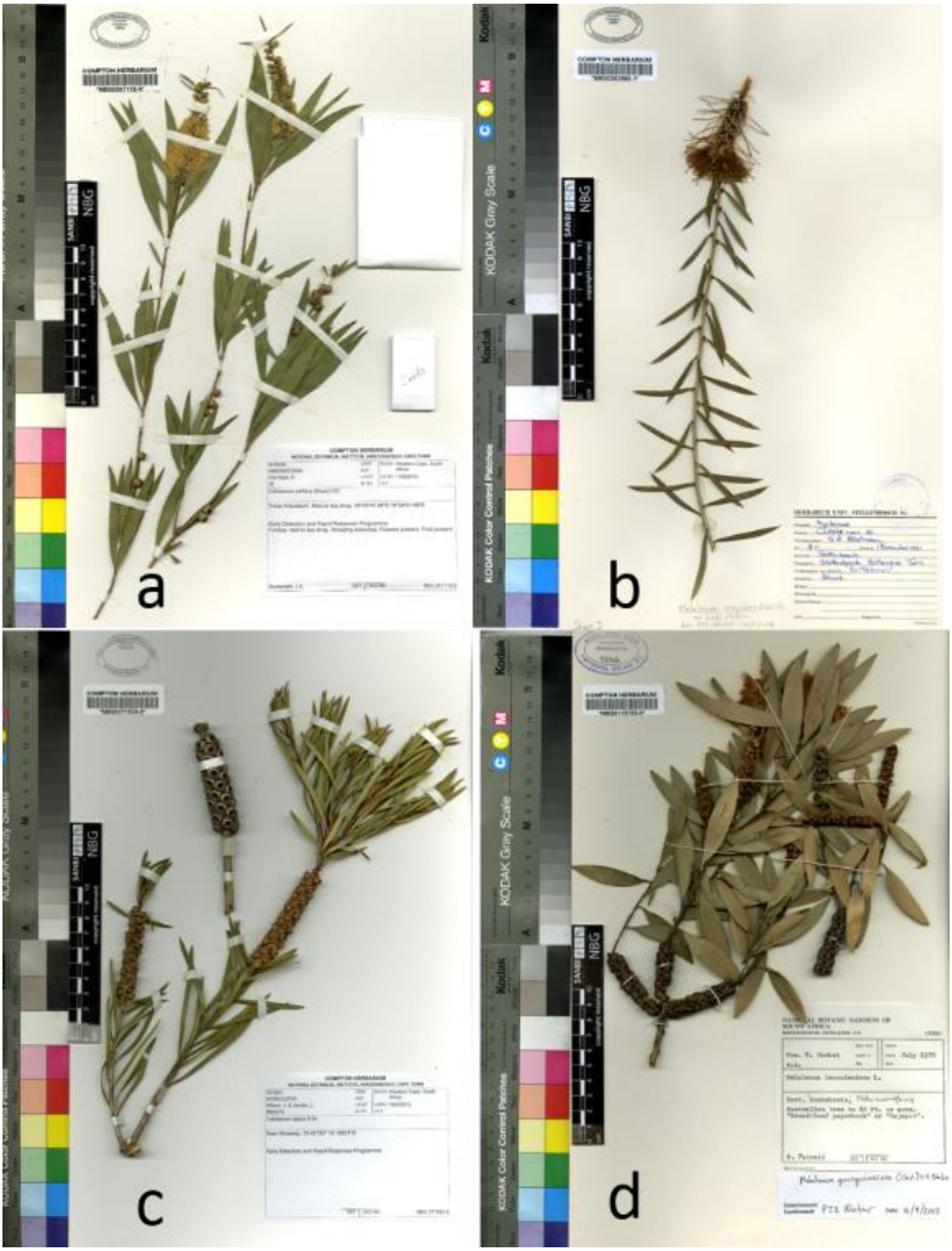

Fig. 4.1. Examples of the types of errors found on the herbarium specimens examined, a) Misidentification: *Melaleuca salicina* misidentified as *Callistemon pallidus*, b) Improved identification: *Callistemon* sp. was further identified as *Melaleuca rugulosa*, c) Synonymy: *Callistemon rigidus* is a synonym of *C. linearis* but is currently accepted as *Melaleuca linearis* var. *linearis*, and d) unresolved taxonomy: prior to 1968, *Melaleuca quinquenervia*, along with several other broad-leaved species were included under *M. leucadendra* sensu lato**.**

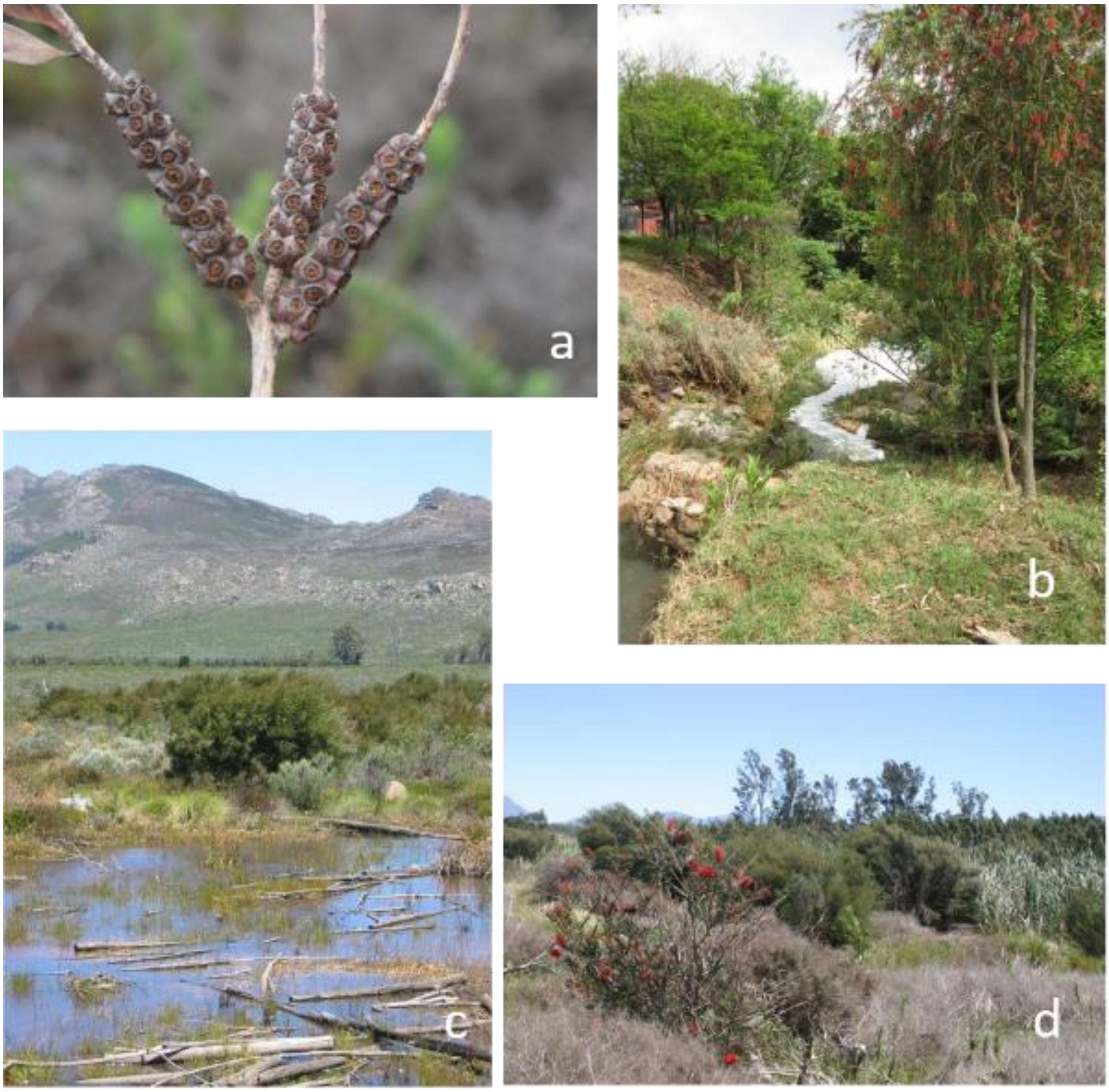

Fig. 4.2. Examples of naturalized *Melaleuca* species in South Africa: a) naturalized *M. quinquenervia* plant showing seed capsules opening after fire; b) *M. viminalis* subsp. *viminalis* naturalized along a stream in an urban setting, c) *Melaleuca parvistaminea* invading a conservation area that was previously under pine plantation, and d) *M. linearis* var. *linearis* is invasive at another site previously under plantation with *M. parvistaminea* in background.

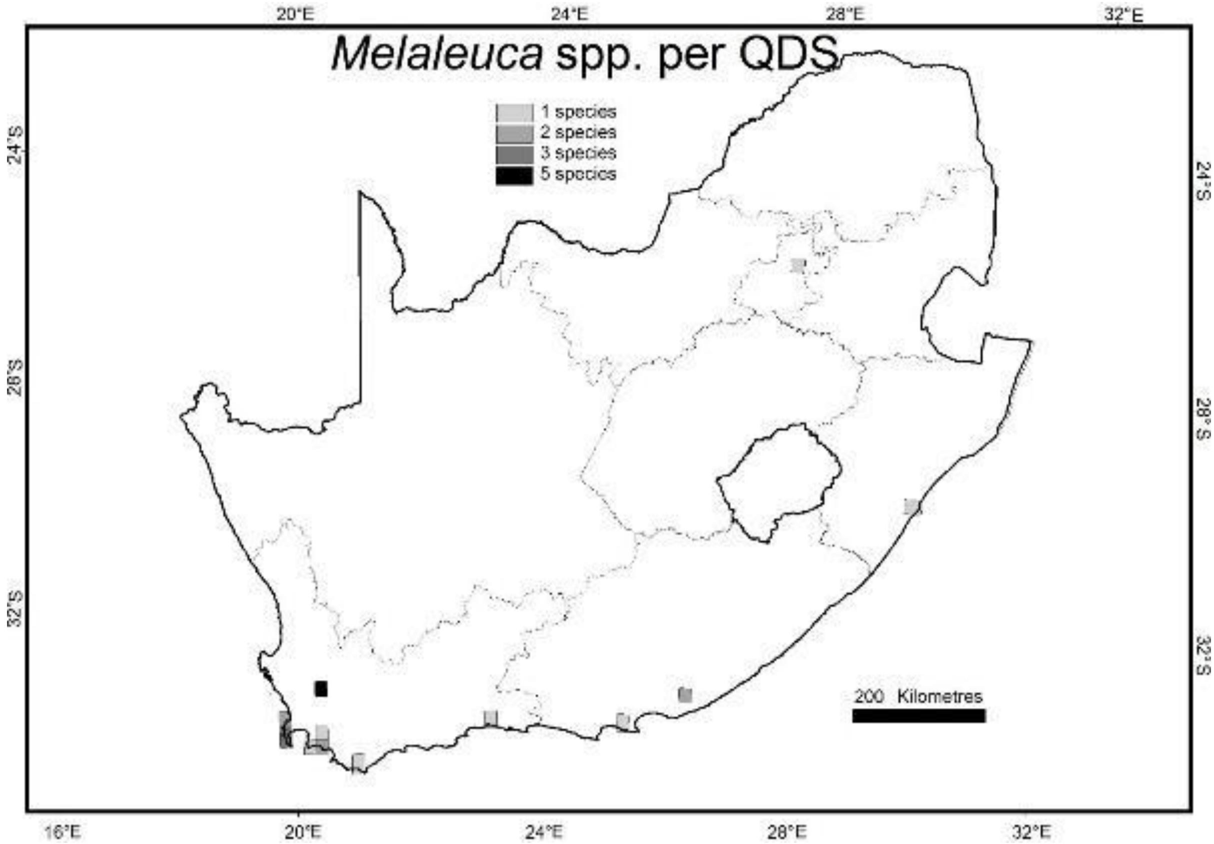

Fig. 4.3. Localities of naturalized *Melaleuca* species in South Africa at the resolution of quarter-degree cells. Darker shading indicates a higher number of species. Grey borders are province boundaries.

4.3.2 List compilation

Our analysis of herbarium specimens and the lists in Glen (2002), also based on herbarium collections, is summarised in Table 4.2 (no additional species were found in Poynton's (2009) list), with species that did not have confirmed herbarium records discussed in Table 4.3. Thirty-six species are confirmed present in South Africa, of which ten species are naturalized – five of these are invasive (Fig. 4.2; Table 4.2). Five naturalized species were categorised as C3 according to Blackburn et al. (2011), indicating that individuals were surviving, reproducing and populations were self-sustaining, but less than 100 m from planting sites (Richardson et al., 2000; Wilson et al., 2014a). *Melaleuca linearis* var. *linearis, M. hypericifolia, M. rugulosa* and *M. viminalis* subsp. *viminalis* are invasive, surviving and reproducing a significant distance from the site of original introduction, but not over a wide extent (D2). *Melaleuca parvistaminea* is invading several sites (E) near the towns of Tulbagh and Wolseley in the Western Cape province (Fig. 4.2c). There are a few separate invasive populations spread over ~10,000 ha, with a total of around 30 000 plants (Fig. 4.3).

Table 4.2
List of 36 *Melaleuca* species in South Africa for which there is a confirmed herbarium record in either the Compton Herbarium, Kirstenbosch (NBG) or in the cultivated collection in the National Herbarium (PRE). Note that several other collections were searched, but no additional species could be discovered. Invasive status is according to Blackburn et al. (2011), with interpretation for trees from Wilson et al. (2014a). All species were used as ornamentals although older records are often associated with historic forestry sites and arboreta. Later records were sourced mainly from gardens and nurseries. Recently used synonyms are listed and are intended to aid recognition of some species.

***Melaleuca* taxon**	**Recently used synonym / misapplied name**	**Earliest record**	**Status in South Africa**	**Notes and references**
M. alternifolia (Maiden & Betche) Cheel		1974	Introduced B2	
M. armillaris (Sol. ex Gaertn.) Sm. subsp. *armillaris*		1930	Naturalized C3	Widely cultivated ornamental. Potentially invasive.
M. brachyandra (Lindl.) Craven	*Callistemon brachyandrus* Lindl.	1968	Introduced B2	
M. bracteata F.Muell.		1981	Introduced B2	
M. citrina (Curtis) Dum.Cours.	*Callistemon citrinus* (Curtis) Skeels	1932	Naturalized C3	Bromilow (2010). Cultivars and hybrids also introduced. Cited in Rejmanek and Richardson (2013). Also recorded in Southern African Plant Invaders Atlas at Honingklip farm (3419AC) in 1998, but plants have been removed
M. cuticularis Labill.		1902	Introduced B2	
M. decora (Salisb.) Britten	*M. genistifolia* Sm.	1963	Introduced B2	
M. decussata R.Br.		1954	Introduced B2/B3	
M. diosmifolia Andrews		1933	Introduced B2	
M. elliptica Labill.		1963	Introduced B2	Observed in Deer park on the slopes of Devil's Peak, Table Mountain, Cape Town. Possibly naturalized, but no supporting evidence.
M. flammea Craven	*Callistemon acuminatus* Cheel	1986	Introduced B2	
M. fulgens R.Br.		1952	Introduced B2	
M. huegelii Endl. subsp. *huegelii*		1945	Introduced B2	

Melaleuca taxon	Recently used synonym / misapplied name	Earliest record	Status in South Africa	Notes and references
M. hypericifolia Sm.		1902	Invasive D2	Hickley et al. (2017). Field data at Hout Bay indicate spread > 100 m.
M. incana R.Br. subsp. *incana*		1967	Introduced B2	
M. incana subsp. *tenella* (Benth.) Barlow		1981	Introduced B2	
M. lanceolata Otto		1982	Introduced B2	
M. lateritia A.Dietr.		1954	Introduced B2	
M. linariifolia Sm.		1958	Introduced B2	
M. linearis Schrad. & J.C.Wendl. var. *linearis*	*Callistemon linearis* (Schrad. & J.C.Wendl.) Colvill ex Sweet, *C. rigidus* R.Br.	1902	Invasive D2	Several plants found at Kluitjieskraal and 56 plants (30–130 cm height range) were found at two sites in Grahamstown.
M. nesophila F.Muell.		1967	Introduced B2	
M. nodosa Sm.		1961	Introduced B2	
M. pachyphylla (Cheel) Craven	*Callistemon pachyphyllus* Cheel	1983	Introduced B2	
M. paludicola Craven	*Callistemon sieberi* DC.	2011	Introduced B2	
M. parvistaminea Byrnes		1933	Invasive E	Invading a wetland system, Jacobs et al. (2014). Misidentified as the morphologically similar *M. ericifolia* Sm.
M. phoenicea (Lindl.) Craven	*Callistemon phoeniceus* Lindl.	1981	Introduced B2	
M. quinquenervia (Cav.) S.T.Blake	*M. leucadendra* L.	1928	Naturalized C3	Jacobs et al. (2015)
M. rhaphiophylla Schauer		1984	Introduced B2	
M. rugulosa (Schltdl. ex Link) Craven	*Callistemon rugulosus* (Schltdl. ex Link) DC.	1961	Invasive D1/D2	Devil's Peak, Cape Town. Spread > 500 m. ~20 adults. Seedlings growing in firebreak.
M. salicina Craven	*Callistemon salignus* (DC.) Colvill ex Sweet	1932	Naturalized C3	

***Melaleuca* taxon**	**Recently used synonym / misapplied name**	**Earliest record**	**Status in South Africa**	**Notes and references**
M. squarrosa Donn ex Sm.		1994	Introduced B2	
M. styphelioides Sm.		1902	Naturalized C3	145 plants at Kluitjieskraal near the town Wolseley (60-450 cm height range)
M. subulata (Cheel) Craven	*Callistemon subulatus* Cheel	2013	Introduced B2/Naturalized C3	Near water body 10km NE of Villiersdorp, possibly at Rockview Dam near Grabouw
M. teretifolia Endl.		1967	Introduced B2	
M. thymifolia Sm.		1907	Introduced B2	
M. viminalis (Sol. ex Gaertn) Byrnes subsp. *viminalis*	*Callistemon viminalis* Sol. ex Gaertn subsp. *viminalis*	1948	Invasive D2	Widely planted with several localized sites of naturalization. Spreading along Kaaimans river ~3 km East of George

Table 4.3
Melaleuca taxa recorded in South Africa for which there is no confirmed herbarium record.

***Melaleuca* taxon**	**Earliest record**	**Source of information**	**Notes**
M. hamulosa Turcz.	Unknown	Glen (2002)	No specimens found in PRE cultivated collection
M. glauca (Sweet) Craven [recorded as *Callistemon speciosus* (Sims) DC.]	Unknown	Glen (2002)	No specimens found in PRE cultivated collection
M. paludosa (Sweet) Craven [recorded as *Callistemon glaucus* (Bonpl.) Sweet]	1979	South African Plant Invaders Atlas (SAPIA)	Probably a misidentification. The only species found at the reported locality in Grahamstown is *M. linearis*.
M. pauperifolia F.Muell.	Unknown	Glen (2002)	No specimens found in PRE cultivated collection
M. wilsonii F.Muell.	1998	South African Plant Invaders Atlas (SAPIA, Australia's Virtual Herbarium (MEL 2053098A)	Land owner at Honingklip near Botrivier in the Western Cape reports historic occurrence of "bottlebrushes" but no *Melaleuca* species occur at this site as of 2011.
M. nervosa (Lindl.) Cheel	Unknown	Gibbs (1998)	One tree recorded at Damara Farm near Malmesbury. Several *Acacia* species trials were also carried out at this site

4.4 Discussion and Conclusions

There are a number of ways that errors can be generated in compilation of species lists (McGeoch et al., 2012), but here we show the challenges that exist at a fundamental stage of the listing process. Importantly, since only a subset of herbaria were analysed in detail, there could be additional errors (and in fact additional species) present in South Africa. The high proportion of misidentifications (Table 4.1) is concerning, indicating the difficulties encountered when dealing with novel species and highlighting the need for expertise on specific non-indigenous taxa. Synonymy, however, does not necessarily imply human error, but rather that use of an outdated or otherwise superseded taxonomy can lead to errors in interpretation, or incorrect estimates of numbers by subsequent users (McGeoch et al., 2012). In this study however, synonymy arose rather from differing perceptions of *Callistemon*, than from human error. Although the effect of synonymy is potentially large (McGeoch et al., 2012), the checking of synonymies is commonly practised. However, a rudimentary training in taxonomic principles is necessary for any practitioner dealing with scientific names. It is of concern that the inclusion of *Callistemon* in an expanded *Melaleuca* is still under debate. All synonym issues found in our study required at least the genus name to be updated. Lists not taking this into account could generate errors of a greater magnitude than errors relating only to the specific epithet.

Lists therefore require the application of taxonomic expertise on taxa not native to a particular region (Pyšek et al., 2013). The knowledge generated from these lists form the basis for informing end users, (e.g. quarantine officials, conservation agencies) that perform crucial functions in stemming the tide of biological invasions and informing future research (e.g. identifying biological control agents) requiring accurate species identifications. Herbaria have often served as barometers for new and rediscovered alien plant species. They also provide a reference source for research or conservation initiatives that require accurate species names. The ongoing decline of resources being allocated to the maintenance of herbaria worldwide will adversely affect many research fields including invasion biology (Guerin, 2013, Pyšek et al., 2013). We strongly believe that part of the funding for invasive species management needs to be allocated to the maintenance and functioning of herbaria and other collections as they are an essential resource for the work (this has begun to be supported in South Africa but further sustained resources need to be devoted to this). The same could be suggested for other fields of botanical research.

While genetic verification of species identifications is proving to be a reliable means of verifying a species, classical taxonomy still remains crucial to the identification of new species to a region (Pyšek et al., 2013). In the absence of molecular data suitable for use in species identification, identifications based on morphology are usually adequate (Pyšek et al., 2013). For these reasons, and an uncertain taxonomy in some cases, we found morphological identification based on published descriptions and keys the best approach to reviewing herbarium specimens of *Melaleuca*. Because suitable molecular data is often lacking, we recommend that DNA barcoding efforts should prioritise potentially invasive genera, so that species can be accurately identified in regions where expertise on that group is likely absent. Species identification issues due to uncertain or unresolved taxonomy can be avoided by continued taxonomic research (Edwards et al., 2010). This research will likely be conducted in the country of origin and therefore cross-border communication and collaboration between taxonomists are essential (Smith et al., 2008, Pyšek et al., 2013). Errors could be avoided by either collaborating with researchers from regions where alien species are native, thus tying into a strategic response of the *Global Invasive Alien Species Strategy* (McNeely, 2001) or by investing in local taxonomic expertise on key alien groups. There are several ways in which these groups could be identified based on known patterns of invasion. Longest residence time, invasiveness in other regions and weedy species are data obtainable from herbarium specimens and could thus be used to identify these groups.

Identification errors noted in this study have had direct implications. *Melaleuca parvistaminea* was initially misidentified in 2011 as the morphologically similar *M. ericifolia* (Jacobs et al., 2014; S2.1). *Melaleuca parvistaminea* was only formally described in 1984 and collections prior to this were treated within the broad concept for *M. ericifolia* (Albrecht, 1987). Some *M. armillaris* subsp. *armillaris* specimens were also misidentified as *M. ericifolia* (e.g. NBG0269364). *Melaleuca ericifolia* is regarded as being predominantly clonal rather than reseeding. This affected management actions, through unforeseen profuse recruitment via seed after clearing and the absence of clonal spread and resprouting (Jacobs et al., 2014). The incorrect name was perpetuated into Richardson and Rejmánek' s (2011) global list of invasive trees and shrubs, but hereafter corrected in an update of this list (Rejmánek and Richardson, 2013). Although this was not investigated, it is possible that publications citing *Melaleuca* species from Richardson and Rejmánek (2011) could carry this mistake forward.

Effective pre-emptive control efforts rely heavily on whether alien species are listed as invasive in that region or are known to be invasive elsewhere (Mack, 1996). As a result of debate surrounding generic limits in the tribe Melaleuceae, especially regarding the recognition of *Callistemon* as a segregate genus (Craven, 2006; Udovicic and Spencer, 2012; Edwards et al., 2010; Craven et al., 2014), species lists included in the recently published *Alien and Invasive Species Regulations in South Africa* (DEA, 2014) may generate errors due to synonymy issues. For example, the regulations list *Callistemon rigidus*, which is now treated as a synonym of *C. linearis* if one accepts the separation of the two genera (see Council of Heads of Australasian Herbaria, 2016); if a broad concept of *Melaleuca* is adopted, then the taxon should be listed as *Melaleuca linearis*. Moreover, several species have been omitted from the regulations, e.g. *Melaleuca parvistaminea,* a species which is clearly invasive and poses a considerable environmental threat (Jacobs et al., 2014). Recognition of situations like these requires adequate taxonomic expertise and familiarity with the group in question.

Hybridization and horticultural selection for some *Melaleuca* species, especially those in the *Callistemon* group can further complicate accurate identification (Brophy et al., 2013). Hybrids and several cultivars exist for some taxa and it is not clear whether some hybrids or cultivars are more invasive than others. Moreover, some *Melaleuca* species, such as *M. linearis*, are apomictic and may further contribute to species identification problems.

We identified ten species of *Melaleuca* naturalised in the Western Cape province of South Africa, but invasions of taxa in this genus are at an early stage, and there is likely to be a high level of invasion debt (sensu Rouget et al., 2016). Unlike other invasive Australian tree and shrub species (e.g. *Acacia* and *Eucalyptus*), *Melaleuca* species were never widely disseminated in South Africa for forestry or dune stabilisation. *Melaleuca quinquenervia* was introduced and widely disseminated for a variety of reasons, including ecosystem engineering, in the USA (Dray et al., 2006). No wide scale plantings took place in South Africa. *Melaleuca* introductions and plantings in South Africa have been for ornamental purposes, mostly in the last few decades. Because naturalized populations are still small there is still the opportunity to eradicate several species if action is taken quickly and with sufficient resources. Besides the small populations, other factors that suggest that eradication is feasible are the short-lived serotinous seed banks, the effectiveness of available herbicides (Jacobs et al., 2014; van Wyk and Jacobs, 2015), limited dispersal capability and a focused, national programme with a mandate to manage emerging invasive species (Wilson et al., 2013). The high level of errors in identification which we found in this study, however, highlights the urgent need to assess and improve the accuracy of alien species lists.

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Chapter 5: Traits associated with naturalization and invasion success in *Melaleuca* (Myrtaceae) species in South Africa

This chapter is presented in the form of a manuscript for submission to a journal.

Author contributions:

LEOJ, DMR, JRUW: Planned the study

LEOJ: Collected data, did all statistical analyses and wrote the first draft of the paper

DMR, JRUW: Edited the manuscript

JRW: Provided guidance on statistical analyses

Abstract

Species, biogeographical and human usage traits have been shown to discriminate between naturalised and invasive species, but often generalisations are limited to a particular group of species. To improve prediction of which *Melaleuca* species could become naturalized or invasive I assessed a variety of traits for 36 *Melaleuca* species in South Africa. I collected information on traits that reflect species characteristics, biogeographic and human usage patterns, and analysed various factors to determine which were associated with naturalisation and invasiveness using generalised linear models. Residence time in South Africa is strongly associated with naturalisation and invasion success, indicating that an invasion debt for the 26 non-naturalized species might exist. With such relatively recent introductions and so few invasions globally in the group it is too early to tell if there are other robust correlates of invasiveness that might emerge with time.

Keywords: Biological invasions; *Callistemon*; Myrtaceae; native range size; residence time; species traits; tree invasions

5.1 Introduction

Finding a consistent set of species traits associated with invasiveness has been described by some authors as the 'silver bullet' in plant invasion ecology (e.g. Rejmánek and Richardson, 1996; Grotkopp and Rejmánek, 2007; Castro-Díez et al., 2011). Identifying such traits would allow us to understand and predict which species would become in invasive and improve our ability to assign risk for functional or taxonomic groups that share particular traits. Baker (1965) proposed a list of characteristics (e.g. fast growth, short juvenile period) that an "ideal weed" would possess. Although much insight was gained from this work, Baker's traits were considered simplistic, as subsequent studies have struggled to consistently link the same traits across taxa and situations (Crawley, 1987; Pyšek and Richardson, 2007; Hayes and Barry, 2008). More recently, as data availability for multi-species comparisons improved, some general patterns have emerged. Pyšek and Richardson (2007) reviewed these studies and found that some traits, like vigorous growth, efficient dispersal, earlier and longer flowering and higher specific leaf area among others, were consistently linked to invasiveness across many plant taxa.

Plant invasion is a process consisting of different stages. This is known as the introduction-naturalization-invasion (INI) continuum where plant species are first introduced to a new biogeographic region, then produce self-sustaining populations before spreading (Blackburn et al., 2011). Alien taxa can cause impacts at any of these stages, but the magnitude of impact increases with the size of the invaded range (Parker et al., 1999). Many recent studies have highlighted that different traits are important at different stages of the INI continuum (see Richardson and Pyšek (2012) for a review). McGregor et al. (2012) compared the importance of different species, biogeographic and human usage traits for introduction and naturalization of pines in Great Britain and New Zealand. Human usage was found to be an important determinant of introduction in both regions and for naturalization in New Zealand, but biogeographic factors was most significant in naturalization of pines in Great Britain (McGregor et al., 2012). Procheş et al. (2012) found similar results supporting the notion that human factors strongly influence patterns of introduction and naturalization in the genus *Pinus*. Several studies have also shown that species that have a longer residence time in a new region are more likely to become naturalised and invasive (Wilson et al., 2007; McGregor et al., 2012; Pyšek et al., 2015).

For Australian *Acacia* species, Gallagher et al. (2011) investigated various traits and found that three out of eight traits studied were important—invasive species were taller, had larger native range sizes and tolerated a wider range of annual precipitation. Morris et al. (2011) linked important ecophysiological traits with the competitive advantage of invasive acacias over native species globally. Invasive acacias become dominant because of interplay between higher growth rates, biomass, water and nutrient acquisition efficiency. In this regard, pines and Australian acacias can be considered model groups for studying traits associated with invasions (Richardson and Rejmánek, 2004; Richardson et al., 2011; Kueffer et al., 2013). Each genus has many species, some of which have been introduced to other regions, and subsets of these have naturalised and invaded. Another factor that makes these genera suitable for such analyses is the availability of data on traits for many species. To determine whether the patterns observed for such “model groups” (sensu Kueffer et al., 2013) apply more widely, further analyses are needed.

Although not as widely invasive as acacias and pines, many species in the family Myrtaceae have been moved around the world and widely planted in many regions outside their native ranges. At least 35 species in the family are known to be invasive (Rejmánek & Richardson 2013). In South Africa, several Myrtaceae species are widespread invaders. These include species in the genera *Eucalyptus*, *Eugenia*, *Kunzea*, *Leptospermum*, *Melaleuca*, *Metrosideros*, *Psidium*, and *Syzygium*. Some of these species are already widespread invaders (Forsyth et al. 2004; Nel et al. 2004; Wilson et al. 2014b), but others are recent introductions and have not had enough time to become naturalized or invasive. Unlike the eucalypts which were widely planted for forestry, species in the genera *Eugenia*, *Kunzea*, *Leptospermum*, *Melaleuca*, *Metrosideros* and *Syzygium* have been planted as ornamental trees, although some of these have been used for small scale forestry trials (see

Poynton (2009) for a review of tree plantings in South Africa). Planting for ornamental use creates a very different pathway of introduction and dissemination compared to planting for forestry. Since ornamental plantings generate lower propagule pressure, the lag phase between plantings and naturalization or invasion is likely to be longer (Donaldson et al., 2014a). Since many of the species in these other genera of Myrtaceae are fairly recent introductions, and given the invasiveness of these species or congeners in other parts of the world, it is likely that a substantial invasion debt (sensu Rouget et al., 2016) exists for this group in South Africa.

Several *Melaleuca* (incl. *Callistemon*) species have already naturalised in small populations, especially in the Western Cape (Jacobs et al., 2016). These species have dry-fruits and to some degree abundant, short-lived seeds in common. Dispersal is usually passively by water or wind unlike fleshy-fruited species which can be dispersed longer distances by vertebrates, and for this reason should be considered separately. Some *Eucalyptus* species have become invasive but not on the same magnitude as *Acacia* or *Pinus*, which has had similar introduction histories (Richardson and Rejmánek, 2011). This could be due to limited dispersal, high seedling mortality and lack of compatible ecto-mycorrhizal associations in the introduced region (Rejmánek and Richardson, 2011). The life history strategies of *Eucalyptus* and *Melaleuca* are similar in a number of aspects: short-lived seeds, limited dispersal, reseeding or resprouting post-fire strategies (Rejmánek and Richardson, 2011; Brophy et al., 2013).

Species with larger native range sizes have often been found to be more likely to become naturalized and invasive (Hayes and Barry, 2008; Hui et al., 2011; Lavoie et al., 2013). McGregor et al. (2012) found that pines with larger native ranges were more likely to naturalise. Hui et al. (2014) noted that native range sizes for naturalised and invasive *Acacia* and *Eucalyptus* was positively correlated. Moodley et al. (2013) found that for Proteaceae, an ornamental family, similar traits are important but that some traits are important only at one particular stage. For example, large native ranges and ability to resprout (among others) increase probability of naturalization, but although large range size was also important, tall, serotinous plants with small seeds were deterministic for invasion. Species with larger native ranges would be adapted to a wider range of habitats and conditions that would allow them to be more suited to establishing and spreading in novel environments. Thus investigating this trait for *Melaleuca* would contribute to growing current understanding, allowing comparing and contrasting across a range of taxa.

In this paper, I explore which traits are associated with naturalisation and invasion success in *Melaleuca.*

5.2 Methods

5.2.1 Species lists

In Jacobs et al. (2016), a list of 36 *Melaleuca* species (sensu lato, including *Callistemon*) present in South Africa was compiled. Using criteria from Blackburn et al. (2011) and Wilson et al. (2014a), it was determined that ten species are naturalised and five species are invasive. For the 36 species, I collected data on various traits to determine which combination of traits are associated with naturalization and invasion success. Table 5.1 provides a list of traits, the data type and the sources from which they were derived.

5.2.2 Trait selection

Traits were selected based on species, biogeographic and human usage characteristics (Table 5.1) that had emerged as being important for separating invasive from non-invasive taxa in groups of woody plants in previous studies (e.g. McGregor et al., 2012). Table 5.2 lists the trait data chiefly derived from information in a comprehensive compilation for *Melaleuca* (Brophy et al., 2013). The response variables, INI status, were derived from Jacobs et al. (2016) and are based on the Blackburn et al. (2011) framework. Native range size was measured as extent of occurrence (EOO) and was determined in this chapter.

Table 5.1
List of traits used to distinguish relative importance at different stages of invasion. Data were available for all species (n = 37). Herbarium specimens for *Melaleuca* species examined were from Compton (NBG), KwaZulu-Natal (NH), Bews (NU) and National (PRE) herbaria. These represent the oldest local collections housing *Melaleuca* specimens and were used to determine minimum residence time. Minimum residence time was not available for *M. subulata*. Data from Australia's Virtual Herbarium (AVH) were extracted to determine native range size.

Traits	**Coding or units**	**Source**
Species characteristics		
Inflorescence width	Millimetres	Brophy et al., 2013
Height	Metres	Brophy et al., 2013
Length of flowering period	Number of months, integer	Brophy et al., 2013
Biogeographic		
Native range size	Km^2	AVH, Brophy et al., 2013
Number of habitats	Integer	Brophy et al., 2013
Human usage		
Minimum residence time	Earliest herbarium specimen collected (years) from South Africa, integer	Herbarium specimens in NBG, NH, NU, PRE

5.2.3 Native range size

To estimate range size, I obtained 63227 records for *Melaleuca* from Australia's Virtual Herbarium (AVH: avh.ala.org.au/search) in June 2016. These records included species still recognised as *Callistemon* species and also other synonyms. Synonymous names were updated to the corresponding *Melaleuca* species according to the lists published in Brophy et al. (2013) which recognise all *Callistemon* species as sunk under the genus *Melaleuca*. The list of records was filtered to only include the 36 species that are present in South Africa so that I could evaluate traits associated with this subset. Records for cultivated and hybrid species were removed. Furthermore, records with uncertain identifications, records outside Australia, points in the sea, incorrect authors or with no GPS readings were excluded. Species distributions were checked against those published in Brophy et al. (2013). Where discrepancies existed, points were deleted. These were mostly records in Australia that were not reported in Brophy et al. (2013), due to plantings and/or human-assisted extralimital establishment. Where a taxon present in South Africa had been identified to subspecies or variety level, I excluded any records from AVH that did not specify these. The exception to this is for *Melaleuca fulgens*, for which the taxonomic entity (subspecific level) present in South Africa could not be determined. Records for the subspecies were combined in this case. Thus, 8029 records for the 36 *Melaleuca* species were used for conducting range size analyses. Combined Australian distribution for these species are shown in Fig. 5.1.

To calculate the extent of occurrence for each *Melaleuca* species I used a convex hull method, a widely used method for calculating extent of occurrence (EOO), as per IUCN guidelines for conservation assessments (ref). Coordinates were transformed to the Albers equal-area projection, which is recommended when calculating area across a range of latitudes (Butler et al., 2016). Records were checked against published distributions in Brophy et al. (2013), and then using spatial analyses in the SP package in R (R Development Core Team, 2012), the area of the minimum convex hull per species was computed in km^2. Where distributions extended beyond the Australian continent (e.g. *M. quinquenervia*), the convex hull was only calculated for Australia.

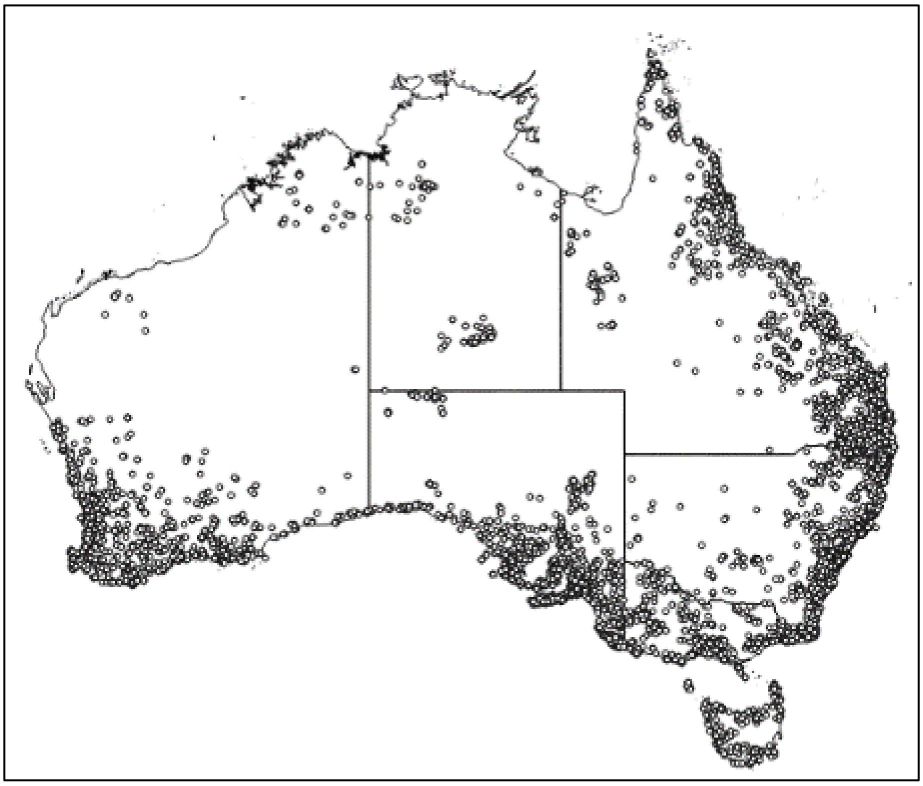

Fig 5.1. Australian native distribution of the 36 *Melaleuca* species present in South Africa

5.2.4 Trait analysis

Trait data were checked for co-linearity. Number of Australian states in which a species occurred was correlated to native range size (0.74) and therefore removed from the analysis. Maximum height is positively correlated (0.6) with native range size, but kept in the analysis, because this was an important determinant in previous studies (e.g. Gallagher et al., 2015). This was to ensure the independence of variables and their relative contribution to the analysis. I used a generalized linear model with binomial errors, using the MASS package in R (R Development Core Team, 2012), to determine if any traits were associated with species that had naturalised or become invasive.

5.3 Results

5.3.1 Trait summary

A list of trait values per species used in the analysis is given in Table 5.2. Native range size (EOO) of all species introduced to South Africa ranged from 9432 km^2 to 5016215 km^2 (examples shown in Fig. 5.2). Mean time in flower is 7.24 months, median minimum residence time is 55 years, mean inflorescence width is 37.27 mm, median number of habitat recorded is four, while mean maximum height is 8.35 m.

5.3.2 Trait analysis

Relative importance of each trait is indicated in Table 5.3. Minimum residence time is an important factor throughout the models for naturalisation and invasion (Fig. 5.3), while number of recorded habitats, inflorescence width and maximum height also play an important role for naturalization.

Table 5.2
List of 36 *Melaleuca* taxa present in South Africa and corresponding trait values. Native range size is defined as the extent of occurrence (EOO, km^2) using convex hull methodology. Introduction-naturalization-invasion status follows Blackburn et al. (2011).

***Melaleuca* taxon**	**INI Status**	**Maximum height (m)**	**Inflorescence width (mm)**	**Minimum residence time (years)**	**Native range size (EOO, km^2)**	**Number of habitats**	**Number of months flowering**	**Native Australian states**
M. alternifolia	Introduced B2	14	25	42	54814.26	3	9	NSW, QLD
M. armillaris subsp. *armillaris*	Naturalized C3	4	20	86	397233.1	4	9	NSW, VIC, TAS
M. brachyandra	Introduced B2	8	35	48	641374.9	3	5	NSW, VIC, SA
M. bracteata	Introduced B2	22	20	35	5016215	5	10	WA, NT, SA, QLD, NSW
M. citrina	Naturalized C3	5	70	84	254983	3	9	NSW, VIC
M. cuticularis	Introduced B2	10	20	114	501840.5	2	6	WA, SA
M. decora	Introduced B2	10	17	53	216424.7	3	3	QLD, NSW
M. decussata	Introduced B2/B3	3	18	62	380040	3	9	VIC, SA
M. diosmifolia	Introduced B2	3	50	83	38874.96	2	3	WA, VIC
M. elliptica	Introduced B2	4.5	65	53	300951.9	2	8	WA
M. flammea	Introduced B2	5	70	30	52010.56	3	3	QLD, NSW
M. fulgens	Introduced B2	3	75	64	995798.5	3	11	WA, NT, SA
M. huegelii subsp. *huegelii*	Introduced B2	5	25	71	48912.94	4	6	WA
M. hypericifolia	Invasive D2	5	60	114	18374.79	3	9	NSW
M. incana subsp. *incana*	Introduced B2	5	15	49	82951.11	4	9	WA, VIC
M. incana subsp. *tenella*	Introduced B2	5	15	35	13539.88	3	3	WA

Melaleuca taxon	INI Status	Maximum height (m)	Inflorescence width (mm)	Minimum residence time (years)	Native range size (EOO, km^2)	Number of habitats	Number of months flowering	Native Australian states
M. lanceolata	Introduced B2	10	23	34	4327903	6	12	WA, SA, VIC, NSW, QLD
M. lateritia	Introduced B2	3	40	62	90947.3	4	9	WA
M. linearis var. *linearis*	Introduced B2	5	65	114	256347.3	3	4	QLD, NSW
M. linariifolia	Invasive D2	10	40	58	1010349	4	5	QLD, NSW
M. nesophila	Introduced B2	3	30	49	9432.19	2	7	WA
M. nodosa	Introduced B2	11	17	55	573345.8	5	8	QLD, NSW
M. pachyphylla	Introduced B2	3	65	33	155356.9	4	12	QLD, NSW
M. paludicola	Introduced B2	8	30	5	809743.2	3	8	QLD, NSW, ACT, VIC
M. parvistaminea	Invasive E	10	11	83	159815.9	5	4	NSW, VIC
M. phoenicea	Introduced B2	6.5	65	35	498451	5	5	WA
M. quinquenervia	Naturalized C3	25	40	88	1196508	6	12	NSW, QLD
M. rhaphiophylla	Introduced B2	10	27	32	207841.4	5	9	WA
M. rugulosa	Invasive D1/D2	5	65	55	400108.2	5	3	SA, VIC
M. salicina	Naturalized C3	15	35	84	251912.6	5	4	QLD, NSW
M. squarrosa	Introduced B2	10	22	22	527078	5	8	NSW, TAS, VIC, SA
M. styphelioides	Naturalized C3	10	24	114	163554.7	4	3	NSW, QLD
M. subulata	Introduced B2/ Naturalized C3	2.5	60	2012	47362.65	5	7	NSW, VIC

Melaleuca taxon	INI Status	Maximum height (m)	Inflorescence width (mm)	Minimum residence time (years)	Native range size (EOO, km^2)	Number of habitats	Number of months flowering	Native Australian states
M. teretifolia	Introduced B2	4	25	49	632989.4	5	4	WA
M. thymifolia	Introduced B2	1.5	25	109	445321.7	6	12	QLD, NSW
M. viminalis subsp. *viminalis*	Invasive D2	35	50	68	3244097	4	12	QLD, NSW, WA

Table 5.3
Statistically significant values (bold) for the generalised linear model (with binomial errors), indicating influence of each trait in determining naturalization (when compared with introduced only) or invasion (when compared with introduced and naturalised) for *Melaleuca* species in South Africa. Model improvement is shown by the Akaike Information Criteria (AIC), where a lower value indicates an improvement as some traits were excluded from the model. Minimum residence time is an important determinant of naturalisation and invasion throughout. Details of the model are given in S5.1.

Status	Minimum residence time	Number of habitats	Inflorescence width	Number of months in flower	Ln(Height)	Ln(Native range size)	AIC
Naturalised	**< 0.001**	**0.012**	**0.005**	0.801	**0.007**	0.375	26.73
	< 0.001	**0.011**	**0.004**	-	**0.004**	0.233	24.8
	< 0.001	**0.023**	**0.007**	-	**0.008**	-	24.22
Invasive	**0.038**	0.426	**0.023**	0.317	0.151	0.694	31.49
	0.024	0.444	**0.024**	0.246	0.16	-	29.64
	0.033	-	**0.031**	0.247	0.078	-	28.23
	0.034	-	0.057	-	0.136	-	27.57

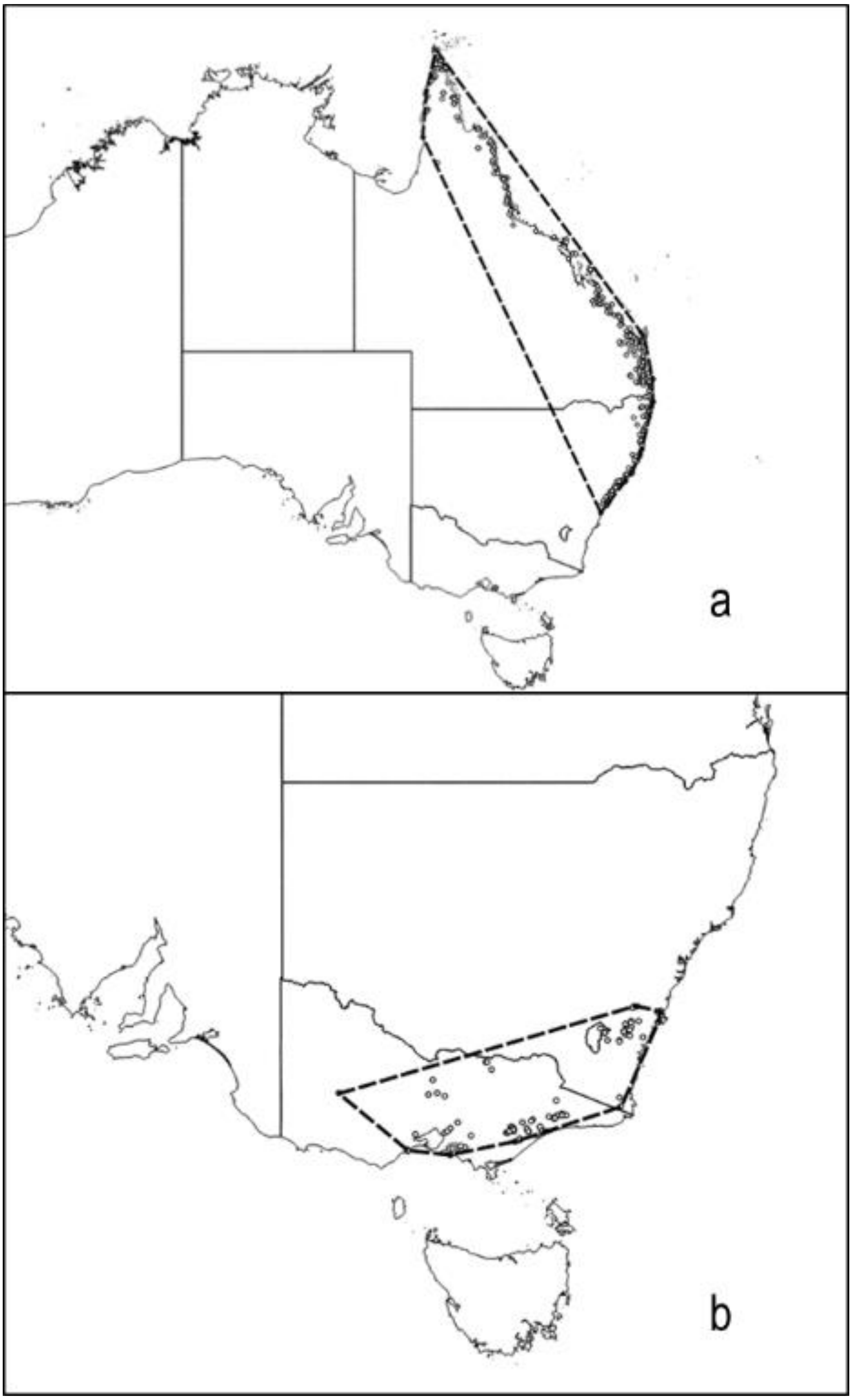

Fig 5.2. Australian native distribution of the (a) naturalised *Melaleuca quinquenervia* and (b) the invasive *Melaleuca parvistaminea* in South Africa. Convex hulls (EOO) are indicated by dashed lines.

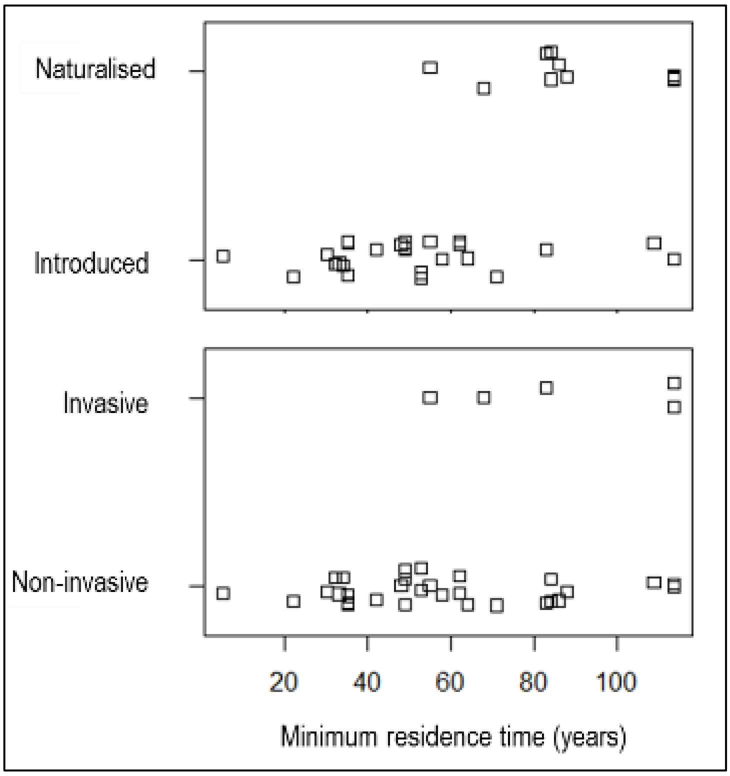

Fig 5.3. Relationship between invasion/naturalization and residence time, indicating that *Melaleuca* species that have been in South Africa for longer have a greater chance of naturalizing and becoming invasive

5.4 Discussion

Longer residence time in a region has been consistently found to be associated with the likelihood that a species has naturalised and invaded novel habitats (Wilson et al., 2007). It is therefore no surprise that for *Melaleuca* species, there is a positive relationship between residence time and naturalization and invasion in South Africa (Fig. 5.3). There could be several reasons for this: more time to adapt to a new environment; species introduced earlier have had more time to spread (be it naturally, deliberately by humans, or accidentally by humans); slowly increasing populations (lag phase) now start experiencing exponential growth and are detected more easily. *Melaleuca* species that were introduced to South Africa prior to 1950 were likely to have been part of forestry trials that took place during that period (Poynton, 2009). Thus pre-selection of invasive traits might also account for these species becoming invasive in addition to residence time.

Interestingly, for naturalization, the number of habitats in which a species was recorded also played an important role, but unlike pines, Australian acacias and eucalypts, native range size was not found to be a significant determinant of *Melaleuca* naturalisation and invasion (Hui et al., 2011, 2014; McGregor et al., 2012). This could mean that habitat breadth is more important at finer spatial scales than native range size which is largely influenced by climate at the biome scale. This is consistent with the findings of Jacobs et al. (2014) which suggested that establishment was not governed chiefly by broad-scale climatic patterns but that stochastic events such as fire or brush cutting was responsible for recruitment. Maximum height and inflorescence width also seem to play a role in naturalisation in conjunction with residence time. Gallagher et al. (2015) reports however that greater maximum height was consistently linked with naturalised species becoming invasive in pairwise comparisons corrected for residence time and phylogeny. Although inflorescence width is a species characteristic, humans could also be artificially selecting for larger, showier flowers and could also be seen as a human usage factor. Larger flowers could allow improved competition for pollinators resulting in better seed set, increasing likelihood of naturalisation under favourable conditions. Since *Melaleuca* flowers are not specialised, they would be able to attract any generalist invertebrate pollinator, like bees, in a novel environment.

Although the list of traits analysed in this study is not exhaustive, it includes many traits that have been shown to be associated with naturalization and invasiveness of woody plants in previous studies. Expansion of the trait suite could include functional traits such as seed mass and specific leaf area which have been found to be strongly correlated with naturalization and invasion in several species groups (e.g. *Acacia* in Gallagher et al., 2011, 2015; *Pinus* in McGregor et al., 2012). Whether a species is a resprouter or reseeder may also be important for *Melaleuca*, since these characteristics are key adaptations for survival and persistence in fire-prone environments and may therefore be linked to invasive potential. Jacobs et al. (2014) showed that *M. parvistaminea* establishment was enhanced by fire and cutting/felling of plants which allowed for seed release and consequent establishment into the invaded habitat. A similar pattern has been observed for establishment of *M. armillaris* subsp. *armillaris*, *M. linearis* var. *linearis* and *M. viminalis* subsp. *viminalis* in South Africa. However, with only 10 naturalised taxa, there is currently not much statistical power to test multiple hypotheses.

A multiple regression analysis approach could be used with the expanded suite of traits. With this, one would be able to take into account co-linearity between interrelated variables, disentangle effects of propagule pressure and scale among others. Furthermore a path analysis would allow dependencies among variables to be modelled (e.g. Pyšek et al, 2015). Given the paucity of data in South Africa alone, a global scale study could be conducted. As with other lesser known invasive groups, the availibity of suitable data to conduct these analyses is a concern.

Given the history of introductions of other Australian tree taxa like *Acacia* and *Eucalyptus* to South Africa (Carruthers et al., 2011), I believe that the introduced subset is representative of introductions elsewhere and could be the highest number of *Melaleuca* species introduced to a single region. Thus, even though the findings here are restricted to South Africa, they should have bearing on other regions where these species have been introduced. Moreover, the invasion history of *Melaleuca* species appears to only just be starting, indicating that there might be a significant invasion debt (Rouget et al,. 2016).

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Chapter 6: General discussion, conclusions and recommendations

More than ten percent (36 species) of the ~290 *Melaleuca* species have been introduced to South Africa (Jacobs et al., 2016). Of these 28% have naturalised and 14% (50 % of naturalised species) have become invasive. If one was to consider the "tens" rule (an often cited, and perhaps over generalised prediction of proportions of species becoming naturalised and invasive; Williamson and Fitter, 1996), then this substantial subset of *Melaleuca* introduced to South Africa would indicate that the ability of these species to naturalise and invade is considerable. In comparison, more than 30 % of *Acacia* species have been introduced to regions beyond their native range, 22 % of these have naturalised and 7 % of introductions (32 % of naturalised species) have become invasive (Richardson et al., 2011). For eucalypts, 47 % have been introduced to other regions, 21 % naturalised and 2 % of introductions (10 % of naturalised species) have become invasive (Rejmánek and Richardson, 2011; Hui et al., 2014). Although this study only takes South African introductions into account, the proportions of naturalised and invasive species for *Melaleuca* are larger than expected given that only one species (*M. quinquenervia*) has caused considerable impacts and can be considered a transformer species (sensu Richardson et al., 2000). Because introductions for *Melaleuca* have been more recent and invasions currently small, these findings are timely to inform management of these species, before larger scale impacts are incurred.

In Chapters 2 and 3, the value of early detection and rapid evaluation of *M. parvistaminea* and *M. quinquenervia* populations is highlighted. The recommendation of category 1a (requiring compulsory control) in each case is reasonable and desirable since infestations are small and these species currently present no conflicts of interest. Eradication of the invasive *M. parvistaminea* is feasible given sufficient resources, but clearing of all known areas must be sustained until 2021. The consequence of not doing this would be the re-establishment of populations, especially in the event of fire and indiscriminate brush cutting, which would trigger seed release (Jacobs et al., 2014). Thus funding spent on clearing operations so far would have been wasted and control at a later stage would likely cost considerably more. Unlike several *Acacia* species which have long-lived seed banks and some eucalypt species that are vigorous resprouters, *M. parvistaminea* can be extirpated from known sites in a relatively short time (Panetta et al., 2011a). The *M. quinquenervia* population at Wolseley responded well to herbicide (existing plants were killed) and since 2014 no new plants were seen. Thus even if a *Melaleuca* species is a resprouter, the short-lived canopy stored seed bank allows for fewer follow-up treatments to be undertaken. Like eucalypts, another favourable factor for control is short seed dispersal distances (Rejmánek and Richardson, 2011). Observations of the other naturalised and invasive populations indicate that this management approach could be applied to all *Melaleuca* species if age at first reproduction is taken into account for each species (Serbesoff-King, 2003; Jacobs et al., 2014), with the intention to follow-up before reseeding plants first reproduce. I recommend that all naturalised and invasive species that aren't used in horticulture be listed, and the feasibility of eradication is assessment (and if eradication is feasible, then they would be listed as category 1a, if not category 1b). If a species is widely planted and still of ornamental value, the recommendation is category 3 (i.e. can't be sold or propagated)

(DEA, 2014). Finally, if the demand for any taxa is very strong such that it might be considered a conflict species (Dickie et al., 2015) and listed as category 2 providing appropriate permit conditions can be developed that would reduce the risk of invasions and impacts to acceptable levels (and in particular the threat to riparian areas and wetlands is assessed and carefully monitored).

Early detection has been listed as a key strategy for managing biological invasions (McNeely et al., 2001). This is desirable for several reasons: rapid information dissemination allowing for risk to be assessed elsewhere, rapid response before spread of populations, thus minimising impact, lower eventual costs meaning that more funding will be available for other priorities and surveillance (McNeely et al., 2001). The research in this thesis is therefore a vital contribution to early detection efforts and enables informed risk assessment aided by information on invasive status (Chapter 4) and which traits contribute to naturalisation and invasion (Chapter 5).

Such detection efforts rely on being able to identify taxa. Similarly, risk assessors use invasive species lists in prevention and surveillance programs as part of a strategy for managing biological invasions. The accuracy of identification is therefore crucial to management. The basis for many alien plant species identification is herbarium specimens. A few misidentifications for *Melaleuca* specimens prompted the evaluation of all local collections of *Melaleuca* to be assessed for accuracy (Chapter 4). The large proportion of specimens with incorrect names and the debate around inclusion of *Callistemon* within *Melaleuca*, resulted in errors in the lists published for regulating invasive species in South Africa (DEA, 2014; Jacobs et al., 2016). The findings of this study therefore suggests a review of taxonomically challenging alien taxa, enlisting aid from specialists in species' native regions where possible. Genetic verification of identification is also recommended.

The analysis of traits in Chapter 5 indicate that residence time was the most crucial consideration for determining which species naturalise or invade. Given that at least half of the introductions could have occurred after 1950, some species will likely become naturalised or invasive. Two species (*M. cuticularis* and *M. thymifolia*) with minimum residence time > 100 years have not yet naturalised. These are shorter shrubs (max. height 1.5 m) with smaller flowers (inflorescence width 25 mm), indicating that these traits may also play a role in naturalisation, even though their native range sizes are fairly large (EOO: 501 841 km^2 and 445 322 km^2). Thus unlike Australian acacias and eucalypts (Hui et al., 2014), native range size has less value for predicting ability to naturalise or invade for *Melaleuca*. Exploring more traits previously linked to naturalisation and invasion could further elucidate predictors for *Melaleuca*. Thus this study could be expanded to include all *Melaleuca* taxa to globally explore which factors determine not only naturalisation and invasion, but also introduction. Different methodologies (e.g. boosted regression trees; Elith et al., 2008) could be used to analyse data, while native range size could be measured as area of occupancy either using alpha-hull or grid-based techniques (Hui et al., 2011). For native range size, this would improve the accuracy since the convex hull method is prone to bias (Burgman and Fox, 2003). However, a broader issue is that with only 36 taxa, there is simply not a great deal of statistical power in these tests.

In conclusion, this thesis is a contribution to the study of model groups in invasion biology (Kueffer et al., 2013). The case studies for *M. parvistaminea* and *M. quinquenervia* highlighted the need for early detection and provided practical management guidelines and recommendations for the entire group. Chapter 4 contributed a specimen-based list of *Melaleuca* species present in South Africa that included information on the introduction status for each species. The need for accuracy in invasive species lists was also highlighted with recommendations as to how this could be addressed. The prediction of risk was informed by the traits analysis, emphasizing residence time as a key predictor, while also comparing and contrasting findings in previous studies. Thus this study combines elements informing the management of biological invasions while furthering current knowledge in the field.

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Supplementary Material

References for supplementary material are listed separately under each section and therefore not included in the bibliography on page xxx. Numbering of supplementary material reflects chapter number (e.g. S2.1 refers to Chapter 2)

S2.1: Discussion on initial misidentification of *M. parvistaminea*

The populations in the Tulbagh Valley are likely all *M. parvistaminea* and not *M. ericifolia* as originally thought. Revision of the identification is based on number of stamens, stamen length, leaf length and its reseeding regenerative strategy (S2.2), and has been confirmed by an expert in Australia (B. Lepschi, pers. comm. August 2013). Specimens and photographs identified as *Melaleuca ericifolia* (none as *M. parvistaminea*) were found in Compton Herbarium (NBG) (S2.3). However, none of these specimens (collected in 2011), except those from the Tulbagh-Wolseley area, were *M. parvistaminea*. These are likely *M. armillaris*, a common ornamental species that is clearly distinct from *M. parvistaminea. Melaleuca parvistaminea* was considered a variety of *M. ericifolia* until 1987 and has a similar distribution (Robinson, 2007). Specimens in South African herbaria that were collected prior to 1987 were therefore all identified as *M. ericifolia*, and nomenclature for alien taxa was not regularly updated. Thus, in this instance, taxonomic uncertainty is likely derived from lack of expertise on this group and a lack of awareness of the splitting of *M. ericifolia* in 1987 (Albrecht, 1987).

The proposed change in identification to *M. parvistaminea* was initially based on the plants in the field being reseeders and not clonal, which excludes *M. ericifolia* as a possibility (Robinson et al., 2006; Robinson, 2007). An examination of the morphology confirmed this. The characters distinguishing *M. parvistaminea* from *M. ericifolia* are: 4-7 stamens per bundle, stamens to 4 cm long, flowers with pink petals (observed on buds, Fig. 2.2C), and leaves 4-11 mm long and raised oil glands on the abaxial leaf surface (S2.2). The initial misidentification led to the expectation of low seed viability and primarily clonal spread in the populations (Robinson, 2007). Profuse recruitment and 98.3% mortality of plants after fire at the Waterval site, and seedling cohorts near cut plants at the Kluitjieskraal plantation indicates however that this species primarily regenerates through reseeding; Robinson (2007) reports seed viability of up to 80%. Plants are not likely to invest in both reseeding and clonal strategies (Robinson 2007), thus further supporting the identification as *M. parvistaminea*.

The case of *M. parvistaminea* in South Africa is a good example of the need for correct identifications, and the crucial role of taxonomy in invasion ecology (Pyšek et al., 2013). The initial misidentification as *M. ericifolia* has led to a number of errors. At first we based decisions on incorrect biology (S2.2) (especially lower fecundity) and expected plants to prefer more inundated habitats. This shows how misidentifications can lead to incorrect management practices; Richardson and Rejmánek (2011) listed *M. ericifolia* as an invasive shrub, but have since changed the taxa to *M. parvistaminea* in a recent update of the list (Rejmánek and Richardson, 2013). Invasive species lists are important tools for decision makers to allocate limited resources and to formulate policy and legislation and as such, errors are likely to be compounded when misidentifications are made (McGeoch et al., 2012) having negative consequences for national invasive species management.

More *Melaleuca* and *Callistemon* species are being recorded as naturalised and potentially invasive in South Africa (Wilson et al., 2013); three more *Melaleuca* species at the Kluitjieskraal wetland alone. Correct identification of a species is important for understanding its biology and ecology, which is a prerequisite for evaluating invasiveness. Ideally, taxonomic verification should be supported by molecular data. The lack of appropriate molecular data for this species and in Myrtaceae in general is being addressed according to a review by Grattapaglia et al. (2012), to further understand the phylogeny, phylogeography and taxonomy in the family. Invasions where trees have small, dry seeds that require a period of inundation (e.g. eucalypts) have not been prominent at a global scale. This group includes the genera *Callistemon*, *Eucalyptus*, *Kunzea*, *Leptospermum*, *Melaleuca*, *Metrosideros*, *Psidium* and *Syzygium*. There is a need for a broader assessment of potential invasiveness of this group. The popularity of the group in horticulture in South Africa, and therefore the wide-scale planting and high propagule pressure (important drivers of invasion success), calls for the development of local taxonomic expertise on these taxa in South Africa.

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Wilson, J. R. U., Ivey, P., Manyama, P., Nänni, I., 2013. A new national unit for invasive species detection, assessment and eradication planning. South African Journal of Science 109, 1-13.

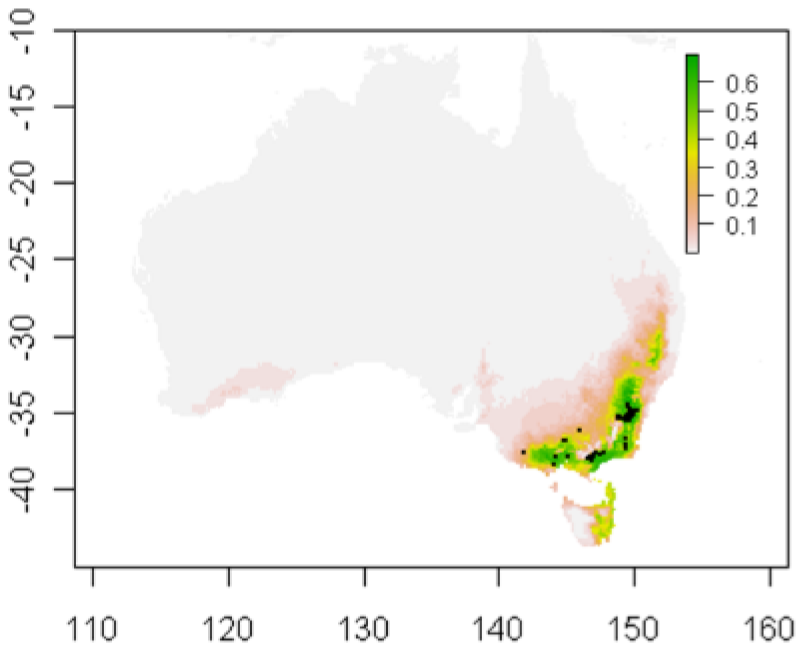
S2.2: Description of *Melaleuca ericifolia* (Wilson, 1991a) and *M. parvistaminea* (Wilson, 1991b) highlighting the key observed differences used to distinguish the two species (bold). Correctly identified *Melaleuca ericifolia* specimens were not available and were therefore not examined; corresponding features are underlined.

	Melaleuca ericifolia Sm. Swamp paperbark	*Melaleuca parvistaminea* Byrnes Rough-barked honey myrtle
Morphological features (http://plantnet.rbgsyd.nsw.gov.au/)	Shrub or small tree to 8 m high with corky bark. Leaves scattered or in whorls of 3, linear, mostly 7–15 mm long, c. 1 mm wide, veins not conspicuous, apex acute, glabrous; petiole to 1 mm long. Inflorescences many-flowered dense spikes 0.7–1.7 cm long; rachis shortly tomentose. Flowers solitary within each bract, white. Petals circular, c. 1 mm long. Stamens 5–7 mm long, 7–13 per bundle; claw to 2 mm long. Fruit cylindrical, 2.5–4 mm diam., orifice 1.5–3 mm diam.; sepals persistent but obscure.	Shrub or small tree to 4 m high with **rough bark**. Leaves scattered or irregularly in whorls of 3, linear, 4–11 mm long, c. 1 mm wide, veins not conspicuous, **oil glands raised**, apex acute to obtuse, glabrous; petiole to 1 mm long. Inflorescences many-flowered dense **spikes 1–2.5 cm long**; rachis shortly tomentose. Flowers solitary within each bract, **white to cream**, **petals often tinged with pink**. Petals broad-ovate to elliptic, to 1.5 mm long. **Stamens 3–4 mm long, 4–7 per bundle**; claw to 0.5 mm long. Fruit cylindrical, c. 3 mm diam., orifice to 2 mm diam.; sepals persistent but obscure.
Regenerative and reproductive features	Rootstock regenerator (asexual)	**Seed-only regenerator** (sexual)
Native distribution in Australia	New South Wales, Victoria and Tasmania	New South Wales and Victoria
Natural habitat preference (Robinson, 2007)	Fresh to brackish swamps with inundation lasting up to a few months	Fresh water swamps with **short-term, intermittent inundation**
Invasiveness elsewhere (http://www.hear.org/gcw/)	"Weed" in Victoria and New South Wales	"Environmental weed" in Victoria and New South Wales

S2.3. Specimens identified as *M. ericifolia* in Compton Herbarium (NBG) that were examined at the start of this study in June 2012.

Identification	**Accession/record number**	**Locality**	**= *M. parvistaminea***	**= *M. ericifolia***	**GPS coordinate**
Melaleuca ericifolia Sm.	NBG0262488	Waterval Nature Reserve	Yes	No	33.34208° S 19.11329° E
Melaleuca ericifolia Sm.	NBG0269364	Next to R340, Willowmore 3323CC	No	No	33.89167° S 23.18699° E
Melaleuca ericifolia Sm.	NBG270001	Somerset West	No	No	34.05022° S 18.83033° E
Melaleuca ericifolia Sm.	NBG0270036	Joostenberg, along Waarburgh Road	No	No	33.83090° S 18.73690° E
Melaleuca ericifolia Sm.	NBG0271362	Cape Agulhas, SANParks	No	No	34.73106° S 19.90667° E

S2.4. *Melaleuca parvistaminea* native distribution in Australia and associated bioclimatically suitable areas (green shading shows most suitable areas), indicating a significant match (AUC=0.998) for the MaxEnt model. This model is projected onto South Africa in Fig. 2.2A.



S2.5. *Melaleuca parvistaminea* pamphlets distributed to land managers asking for sightings. Note the leaflets refer to the species as *M. ericifolia* as they were produced prior to the correct identification being determined.

Front of pamphlet

What does it look like?

Melaleuca ericifolia (Myrtaceae) is a shrub or a small tree, 2–9 m high, with bark tearing off in pieces. **Leaves small, linear, dark green** and scattered or in whorls of three. Inflorescences many-flowered, in dense spikes. Leaves have a camphor smell when crushed. **Flowers small (up to 20 mm long), creamy white in colour** and can be seen from September to November. The fruit is a small cylindrical capsule containing numerous minute seeds.

Why is it important?

Melaleuca ericifolia is a proposed Category 1a invader plant. Under South African legislation, this means that it is prohibited and all existing plants must be eradicated. This alien plant species (native to Australia) grows along watercourses and seasonally inundated wetlands and will form dense thickets in wetlands. This poses a threat to water resources and water dependent biodiversity and related ecosystem services. This species can also tolerate well-drained situations. *Melaleuca ericifolia* can outcompete/exclude indigenous species and thus often form monospecific stands. The Early Detection and Rapid Response Programme (EDRR) is taking a precautionary approach and is in the process of collecting reports of its presence in southern Africa so we can eradicate it from the region before it becomes widespread.

What to do if you see it?

Please report sightings of these plants to the Early Detection and Rapid Response Programme (EDRR) staff at SANBI. Please do not remove any parts of the plant if you find it, as the seeds readily drop out of the fruits. If possible, provide us with a locality description, a photo and a GPS coordinate.

A, *Melaleuca ericifolia* bush about 3 m tall; B, *M. ericifolia* stems showing the rough bark texture; C, *M. ericifolia* flowers, 7–12 mm long. On the cover: *M. ericifolia* seeds.

Contact

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SANBI Graphics
November 2011

Back of pamphlet

S2.6. Evaluation of invasive risk of *Melaleuca parvistaminea* using the Australian Weed Risk Assessment scheme (Pheloung et al., 1999)

Question	Answer	Reference	Score	Range of possible scores
Is the species highly domesticated?	No	van Wyk et al. (2012)	0	0 or -3
Species suited to South African climates	High	Bioclimatic model	2	0, 1 or 2
Quality of climate match data (0—low; 1—intermediate; 2—high)	Intermediate	Bioclimatic model	1	0, 1 or 2
Broad climate suitability (environmental versatility)	No, restricted to SE Australia. temperate, warm summer	Köppen-Geiger climate zones	0	0, 1 or 2
Native or naturalised in regions with extended dry periods	No	WORLDCLIM data	0	0 or 1
Does the species have a history of repeated introductions outside its natural range?	No	Richardson and Rejmánek (2011)	0	0 or 1
Naturalised beyond native range	No	http://www.hear.org/gcw/	0	0, 1, 2, 3 or 4
Garden/amenity/disturbance weed	No		0	0, 1, 2, 3 or 4
Weed of agriculture/horticulture/forestry	No	http://www.hear.org/gcw/	0	0, 1, 2, 3 or 4
Environmental weed	yes	http://www.hear.org/gcw/	4	0, 1, 2, 3 or 4
Congeneric weed	Yes	http://www.hear.org/gcw/	2	0, 1 or 2
Produces spines, thorns or burrs	No		0	0 or 1
Allelopathic	Unknown, but leaves are aromatic and allelopathy is well-known in the family (e.g. *Eucalyptus* spp.)		0	0 or 1
Parasitic	No		0	0 or 1
Unpalatable to grazing animals	?			-1 or 1
Toxic to animals	?			0 or 1
Host for recognised pests and pathogens	No		0	0 or 1
Causes allergies or is otherwise toxic to humans	No		0	0 or 1
Creates a fire hazard in natural ecosystems	Yes, the species can create monospecific stands of large shrubs (> 3 m) not characteristic in natural Breede Shale Renosterveld		1	0 or 1
Is a shade tolerant plant at some stage of its life cycle	Yes, seedlings and adults grow well in shade of pine trees		1	0 or 1
Grows on infertile soils	?			0 or 1
Climbing or smothering growth habit	No		0	0 or 1
Forms dense thickets	Yes		1	0 or 1
Aquatic	No		0	0 or 5
Grass	No		0	0 or 1
Nitrogen fixing woody plant	No		0	0 or 1
Geophyte	No		0	0 or 1
Evidence of substantial reproductive failure in native habitat	No		0	0 or 1
Produces viable seed	Yes		1	-1 or 1
Hybridises naturally	?			-1 or 1
Self-fertilisation	?			-1 or 1
Requires specialist pollinators	No, flowers have generalist characteristics		0	0 or -1
Reproduction by vegetative	No		-1	-1 or 1

propagation				
Minimum generative time (years)	5 yrs		-1	-1, 0, or 1
Propagules likely to be dispersed unintentionally	Yes, by workers or vehicles		1	-1 or 1
Propagules dispersed intentionally by people	No		-1	-1 or 1
Propagules likely to disperse as a produce contaminant	No		-1	-1 or 1
Propagules adapted to wind dispersal	Yes, seeds are small and can therefore be dispersed by wind.		1	-1 or 1
Propagules buoyant	Yes, seeds are small and may be buoyant for short distances		1	-1 or 1
Propagules bird dispersed	No		-1	-1 or 1
Propagules dispersed by other animals (externally)	No, although spread by baboons can't completely be disregarded		-1	-1 or 1
Propagules dispersed by other animals (internally)	No		-1	-1 or 1
Prolific seed production	Yes		1	-1 or 1
Evidence that a persistent propagule bank is formed (> 1 yr)	No		-1	-1 or 1
Well controlled by herbicides	Yes		-1	-1 or 1
Tolerates or benefits from mutilation, cultivation or fire	Yes, seeds are released from serotinous capsules after fire and clearing thus promoting spread	This study	1	-1 or 1
Effective natural enemies present in Australia	No		-1	-1 or 1

References

Pheloung, P.C., Williams, P.A., Halloy, S.R., 1999. A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. Journal of Environmental Management 57, 239-251.

S2.7. Species report for *Melaleuca parvistaminea* (using standardised format suggested by Wilson et al., 2014a)

Species: *Melaleuca parvistaminea* Byrnes (Myrtaceae), (van Wyk 1, NBG-262488). No subspecific information available

Location: South Africa

Status: Invasive; E under Blackburn; not known to be cultivated recently (possibly introduced for arboreta trials before 1990)

Potential: coastal areas of the southern parts of the Western Cape are suitable, but likely establishment depends more on site specific conditions, such a seasonal inundation and fire.

Abundance: ~26 000 plants (2012); 1.15 ha (condensed area); numerous seeds stored on plants in serotinous capsules.

Population Growth Rate: not known, but expansion will be episodic based on recruitment events triggered by fire and water availability

Extent: 2 populations over 1 800 ha

Spread: Unknown, thus far no evidence of long distance dispersal. Dispersal is via wind and water. Still restricted to sites at Kluitjieskraal and Waterval, near the towns of Wolseley and Tulbagh.

Impact: Monoculture created, potential transformer species that uses excessive resources and is a fire promoter (sensu Richardson et al., 2000) For an Australian Weed Risk Assessment 41 of 49 questions answered, score = 9, see Jacobs et al., 2014).

Threat: Not quantified

Survey method(s) used: Systematic walked transects to generate point distributions. Pamphlets were circulated to land owners, herbarium specimens and the spotter website, www.ispot.org.za, were examined, explicit efforts at site delimitation found no plants outside the area.

Notes: eradication plan in place, with an initial estimate that eradication can be declared by 2021 at a cost of ZAR 3 475 000 (US$ 355 400).

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Information compiled by: Llewellyn Jacobs, ljacobs@capenature.co.za

References

Jacobs, L.E.O., Richardson, D.M., Wilson, J.R.U., 2014. *Melaleuca parvistaminea* Byrnes (Myrtaceae) in South Africa: Invasion risk and feasibility of eradication. South African Journal of Botany xxx, xxxx. http://doi.org/10.1016/j.sajb.2014.05.002 .

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Pheloung, P.C., Williams, P.A., Halloy, S.R., 1999. A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. Journal of Environmental Management 57, 239-251.

S3.1. Publicity flyers for *Melaleuca quinquenervia* issued to conservation agencies and land-owners

Front of pamphlet

What does it look like?

Melaleuca quinquenervia is a member of the *Myrtaceae* family (tea trees, honey myrtles or paperbarks) with sister genera such as *Eucalyptus* (gum trees) and *Leptospermum*. It is an evergreen tree that grows up to 35m high, with pale cinnamon to whitish flaking bark. Leaves are grey-green and obovate in shape, have five distinctive parallel veins (except on seedlings) and smell of camphor when crushed. Flowers are creamish-white and arranged in 'bottle-brush' inflorescences 50–100mm long. The species flowers throughout autumn and winter; fruits are small, woody, cylindrical capsules arranged in clusters.

Figure 1.—*Melaleuca quinquenervia* is an evergreen tree 12–35 m tall, with pale cinnamon to whitish, flaking bark.

Figure 2.—Leaves are grey-green, have five distinctive (except on seedlings), parallel veins, and smell of camphor when crushed.

Figure 3.—The species flowers throughout autumn and winter; fruits are small, woody, cylindrical capsules arranged in clusters.

Why is this plant a problem?

Melaleuca quinquenervia is native to Australia, Indonesia, New Caledonia and Papua New Guinea. It is only known to have invaded two sites in South Africa. However, it has invaded 202 000 ha of natural forest, riparian zones, open swamps and wetlands in the Florida Everglades in the United States of America. Between 1989 and 1999, the US government spent US$ 25 million on the control of this species. If left uncontrolled, the species can form monocultures that displace native vegetation. Dense stands of the species are fire-prone. The Invasive Species Programme has taken a precautionary approach and is calling for reports of its presence in southern Africa so that we can control plants before populations of this species become widespread.

On the lookout?

This species prefers to grow in or near streams or salt marshes. Also look out for them in arboreta and commercial forestry exit areas. Please report sightings irrespective of whether the plants are spreading or not.

Where are you likely to see it?

When you see *Melaleuca quinquenervia*, please don't damage or pick any part of the plant because this will encourage the plant to release seeds. Contact the Invasive Species Programme and provide us with the locality description, a photograph and GPS co-ordinates, if possible.

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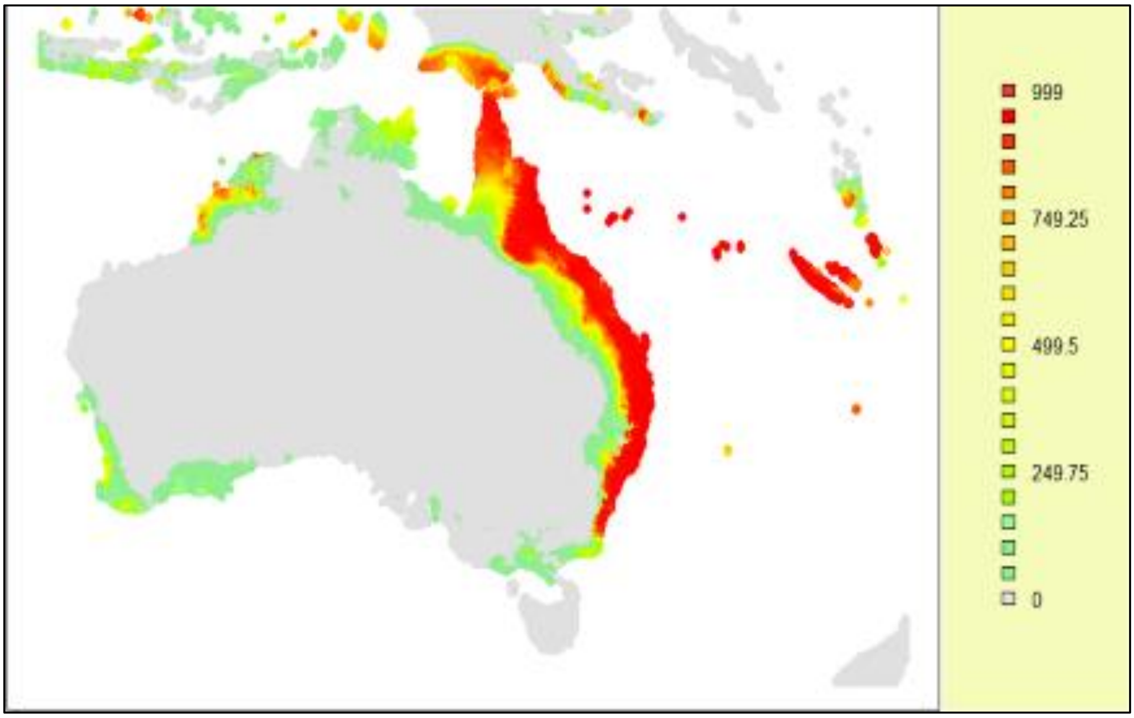
SANBI Publications March 2014

Back of pamphlet

S 3.2. Distribution of *Melaleuca quinquenervia* as predicted by Generalised Additive Model for the native distribution range.



S3.3. Species report for *Melaleuca quinquenervia* in South Africa based on the scheme proposed by Wilson et al. (2014a).

Species: *Melaleuca quinquenervia* (Cav.) S.T. Blake. For identification key, see Craven and Cowie (2013).

Location: South Africa, Table 1 in Jacobs et al. (2015)

Status: Various, at most invasive; E under Blackburn et al. (2011); earliest specimen from 1950.

Global uses: Windbreak; ornament (in South Africa); soil stabilization; erosion control; soil improvement, bees.

Threat: Parts of Limpopo, Mpumalanga and coastal areas along KwaZulu-Natal are at high risk. Wetlands and water courses and areas prone to fire are especially favourable for *M. quinquenervia*. The above ground seed bank is released in response to fire and felling.

Abundance: All populations small with <500 mature individuals before control operations.

Population Growth Rate: Not known

Extent: At least 5 sites, and 3 sites of naturalisation widely dispersed across South Africa. All populations small 2 ha where naturalized at Wolseley, and < 1ha at Tokai.

Spread: Seeds dispersed short-distances by wind. Seeds are buoyant and therefore water dispersed as well. Rates of spread not known, but the origin of several populations appears to be removed from obvious sources of introduction suggesting some dispersal.

Impact: Impact yet to be assessed in South Africa. Serbesoff-King (2003) reviews impacts by *M. quinquenervia* in the USA.

Survey method(s) used: Publicity flyers were distributed to land owners and managers who then reported occurrence. Where naturalized populations occur, systematic, walked surveys were conducted to determine population size and extent.

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Information compiled by: Llewellyn Jacobs (ljacobs@capenature.co.za)

References:

Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V., Wilson, J.R.U., Richardson, D.M., 2011. A proposed unified framework for biological invasions. Trends in Ecology and Evolution 26**,** 333–339.

Craven, L.A., Cowie, I.D., 2013. Taxonomic notes on the broad-leaved paperbarks (Myrtaceae, *Melaleuca*), including the description of one new species from northern Australia and a key to all taxa. Blumea 57, 207-209.

Jacobs, L.E.O., Van Wyk, E., Wilson, J.R.U., 2015. Recent discovery of small naturalised populations of *Melaleuca quinquenervia* (Cav.) S.T. Blake in South Africa. BioInvasions Records 4(1), 53-59.

Serbesoff-King, K., 2003. *Melaleuca* in Florida: A literature review on the taxonomy, distribution, biology, ecology, economic importance and control measures. Journal of Aquatic Plant Management 41, 1-53.

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S 3.4. Australian Weed Risk Assessment for *Melaleuca quinquenervia* in South Africa. With a total score of 21, the species would have been rejected at a pre-border evaluation.

Question	**Answer**	**Reference**	**Score**	**Range of possible scores**
Is the species highly domesticated?	No	Poynton (2009)	0	0 or -3
Species suited to South African climates	Yes	Bioclimatic model	2	0, 1 or 2
Quality of climate match data (0—low; 1—intermediate; 2—high)	High	Atlas of Living Australia (http://www.ala.org.au/)	2	0, 1 or 2
Broad climate suitability (environmental versatility)	Yes	Native range occupies three Koppen-Geiger zones	2	0, 1 or 2
Native or naturalised in regions with extended dry periods	No	Watt et al., 2009	1	0 or 1
Does the species have a history of repeated introductions outside its natural range?	Yes	Watt et al., 2009	1	0 or 1
Naturalised beyond native range	Yes	Watt et al., 2009	2	0, 1, 2, 3 or 4
Garden/amenity/disturbance weed	No	Randall's Global compendium of weeds	0	0, 1, 2, 3 or 4
Weed of agriculture/horticulture/forestry	Yes	this paper	4	0, 1, 2, 3 or 4
Environmental weed	Yes		4	0, 1, 2, 3 or 4
Congeneric weed	No	Rejmanek and Richardson, 2013	0	0, 1 or 2
Produces spines, thorns or burrs	No	Serbesoff-King, 2003	0	0 or 1
Allelopathic	No	Serbesoff-King, 2003	0	0 or 1
Parasitic	No	Serbesoff-King, 2003	0	0 or 1
Unpalatable to grazing animals	No		-1	-1 or 1
Toxic to animals	No		0	0 or 1
Host for recognised pests and pathogens	No		0	0 or 1
Causes allergies or is otherwise toxic to humans	Yes	Serbesoff-King, 2003	1	0 or 1
Creates a fire hazard in natural ecosystems	Yes	Serbesoff-King, 2003	1	0 or 1
Is a shade tolerant plant at some stage of its life cycle	No	Serbesoff-King, 2003	0	0 or 1
Grows on infertile soils	Yes	Serbesoff-King, 2003	1	0 or 1
Climbing or smothering growth habit	No	Serbesoff-King, 2003		0 or 1
Forms dense thickets	Yes	Serbesoff-King, 2003	1	0 or 1
Aquatic	No	Serbesoff-King, 2003	0	0 or 5

Grass	No	Serbesoff-King, 2003	0	0 or 1
Nitrogen fixing woody plant	No	Serbesoff-King, 2003	0	0 or 1
Geophyte	No	Serbesoff-King, 2003	0	0 or 1
Evidence of substantial reproductive failure in native habitat	No		0	0 or 1
Produces viable seed	Yes	Serbesoff-King, 2003	1	-1 or 1
Hybridises naturally	No	Serbesoff-King, 2003	-1	-1 or 1
Self-fertilisation	Yes	Serbesoff-King, 2003	1	-1 or 1
Requires specialist pollinators	No	Serbesoff-King, 2003	0	0 or -1
Reproduction by vegetative propagation	No	Serbesoff-King, 2003	-1	-1 or 1
Minimum generative time (years)	1 year	Serbesoff-King, 2003	1	-1, 0, or 1
Propagules likely to be dispersed unintentionally	No	Serbesoff-King, 2003	-1	-1 or 1
Propagules dispersed intentionally by people	No		-1	-1 or 1
Propagules likely to disperse as a produce contaminant	No		-1	-1 or 1
Propagules adapted to wind dispersal	No		-1	-1 or 1
Propagules buoyant	Yes	Serbesoff-King, 2003	1	-1 or 1
Propagules bird dispersed	No	Serbesoff-King, 2003	-1	-1 or 1
Propagules dispersed by other animals (externally)	No	Serbesoff-King, 2003	-1	-1 or 1
Propagules dispersed by other animals (internally)	No	Serbesoff-King, 2003	-1	-1 or 1
Prolific seed production	Yes	Serbesoff-King, 2003	1	-1 or 1
Evidence that a persistent propagule bank is formed (> 1 yr)	Yes (in the canopy)	Serbesoff-King, 2003	1	-1 or 1
Well controlled by herbicides	Yes	Serbesoff-King, 2003	1	-1 or 1
Tolerates or benefits from mutilation, cultivation or fire	Yes	Serbesoff-King, 2003	1	-1 or 1
Effective natural enemies present in Australia	Yes, not clear	Serbesoff-King, 2003	1	-1 or 1
Total score			**21**	

References

Poynton, R.J., 2009. Tree Planting in Southern Africa: Vol. 3 Other Genera , Department of Agriculture, Forestry, and Fisheries, Pretoria, South Africa

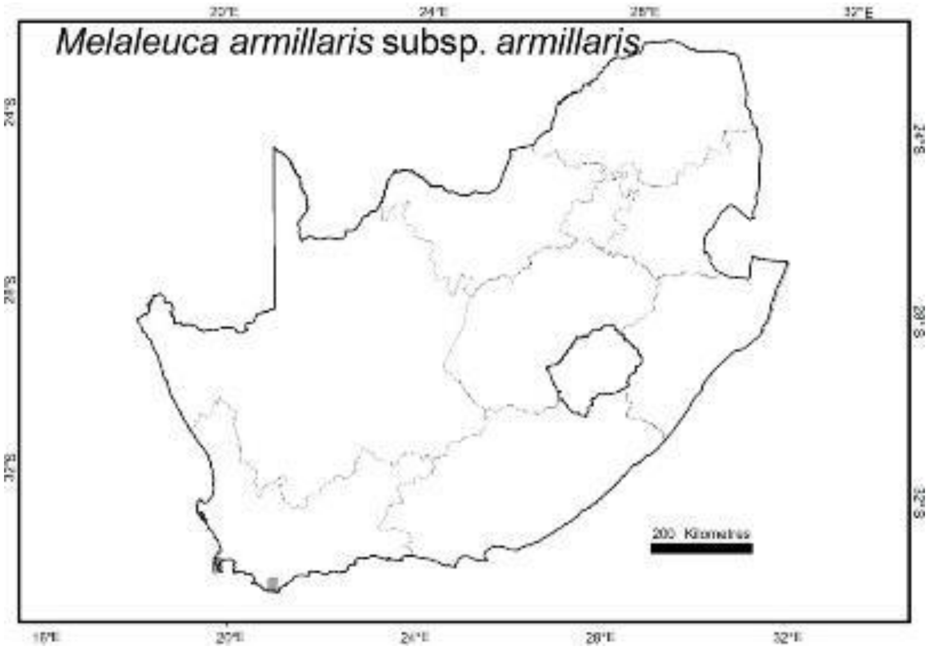
S4.1. Herbarium specimens requiring name changes, indicating types of errors.

Accession number	Label on herbarium specimen	Corrected name	Error type
NBG0275057	*Melaleuca armillaris* Sm.	*Melaleuca armillaris* (Sol. ex Gaertn) Sm. subsp. *armillaris*	Specimen could be further identified
NBG0262486	*Melaleuca armillaris* Sm.	*Melaleuca armillaris* (Sol. ex Gaertn) Sm. subsp. *armillaris*	Specimen could be further identified
NBG0262486	*Melaleuca armillaris* Sm.	*Melaleuca armillaris* (Sol. ex Gaertn) Sm. subsp. *armillaris*	Specimen could be further identified
NBG0262486	*Melaleuca armillaris* Sm.	*Melaleuca armillaris* (Sol. ex Gaertn) Sm. subsp. *armillaris*	Specimen could be further identified
NBG0269804	*Melaleuca armillaris* Sm.	*Melaleuca armillaris* (Sol. ex Gaertn) Sm. subsp. *armillaris*	Specimen could be further identified
NBG0276326	*Melaleuca armillaris* Sm.	*Melaleuca armillaris* (Sol. ex Gaertn) Sm. subsp. *armillaris*	Specimen could be further identified
NBG1457131	*Melaleuca armillaris* Sm.	*Melaleuca armillaris* (Sol. ex Gaertn) Sm. subsp. *armillaris*	Specimen could be further identified
NBG0275059	*Melaleuca deanei* F.Muell.	*Melaleuca armillaris* (Sol. ex Gaertn) Sm. subsp. *armillaris*	Misidentification
NBG0269364	*Melaleuca ericifolia* Sm.	*Melaleuca armillaris* (Sol. ex Gaertn) Sm. subsp. *armillaris*	Misidentification
NBG0270001	*Melaleuca ericifolia* Sm.	*Melaleuca armillaris* (Sol. ex Gaertn) Sm. subsp. *armillaris*	Misidentification
NBG0270036	*Melaleuca ericifolia* Sm.	*Melaleuca armillaris* (Sol. ex Gaertn) Sm. subsp. *armillaris*	Misidentification
NBG0271362	*Melaleuca ericifolia* Sm.	*Melaleuca armillaris* (Sol. ex Gaertn) Sm. subsp. *armillaris*	Misidentification
NBG0262929	*Melaleuca* sp.	*Melaleuca citrina* (Curtis) Dum.Cours.	Specimen could be further identified
NBG0263541	*Callistemon lanceolatus* DC.	*Melaleuca citrina* (Curtis) Dum.Cours. (probable identification)	Synonym
NBG0263544	*Callistemon lanceolatus* DC.	*Melaleuca citrina* (Curtis) Dum.Cours. (probable identification)	Synonym
NBG0263539	*Callistemon lanceolatus* DC.	*Melaleuca citrina* (Curtis) Dum.Cours. (probable identification)	Synonym
NBG0263538	*Callistemon lanceolatus* DC.	*Melaleuca citrina* (Curtis) Dum.Cours. (probable identification)	Synonym
NBG0269420	*Callistemon rigidus* R.Br.	*Melaleuca citrina* (Curtis) Dum.Cours. (probable identification)	Misidentification
NBG0269889	*Callistemon rigidus* R.Br.	*Melaleuca citrina* (Curtis) Dum.Cours. (probable identification)	Misidentification
NBG0270647	*Callistemon rigidus* R.Br.	*Melaleuca citrina* (Curtis) Dum.Cours. (probable identification)	Misidentification
NBG0263540	*Callistemon* sp.	*Melaleuca citrina* (Curtis) Dum.Cours. (probable identification)	Specimen could be further identified
NBG0270455	*Callistemon viminalis* (Sol. ex Gaertn) G.Don	*Melaleuca citrina* (Curtis) Dum.Cours. (probable identification)	Misidentification
NBG0275063	*Melaleuca ericifolia* Sm.	*Melaleuca cuticularis* Labill.	Misidentification
NBG0275064	*Melaleuca ericifolia* Sm.	*Melaleuca cuticularis* Labill.	Misidentification
NBG0275065	*Melaleuca ericifolia* Sm.	*Melaleuca cuticularis* Labill.	Misidentification
NBG0275062	*Melaleuca ericifolia* Sm.	*Melaleuca cuticularis* Labill.	Misidentification
NBG0275068	*Melaleuca leucadendra* L.	*Melaleuca cuticularis* Labill.	Misidentification

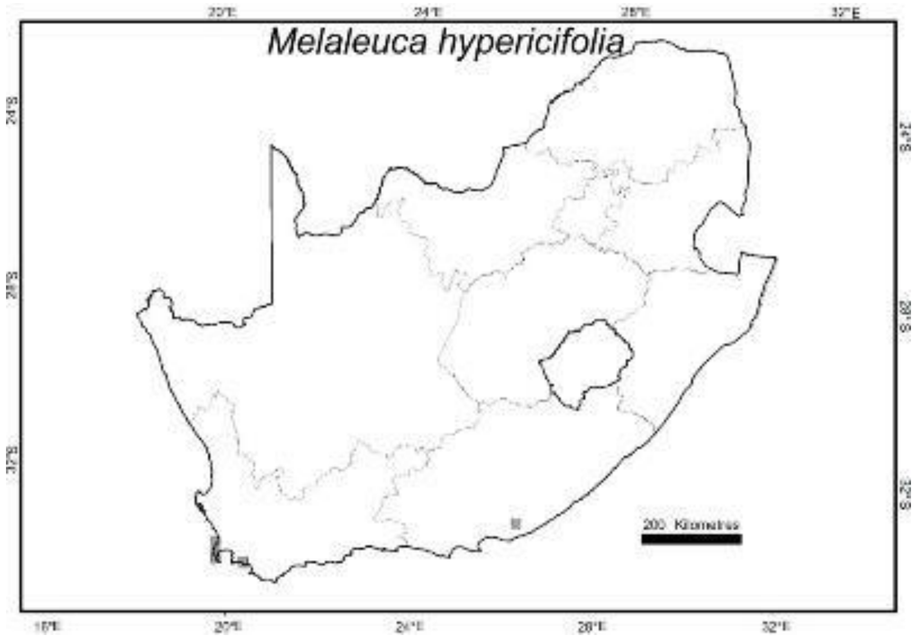
Accession number	Label on herbarium specimen	Corrected name	Error type
NBG0269293	*Melaleuca* sp.	*Melaleuca huegelii* Endl. subsp. *huegelii*	Specimen could be further identified
NBG0117547	*Melaleuca incana* R.Br.	*Melaleuca incana* R.Br. subsp. *incana*	Specimen could be further identified
NBG0270305	*Melaleuca quinquenervia* (Cav.) S.T.Blake	*Melaleuca linariifolia* Sm.	Misidentification
NBG0262925	*Melaleuca* sp.	*Melaleuca linariifolia* Sm.	Specimen could be further identified
NBG0262926	*Melaleuca* sp.	*Melaleuca linariifolia* Sm.	Specimen could be further identified
NBG0271524	*Callistemon rigidus* R.Br.	*Melaleuca linearis* Schrad. & J.C.Wendl. var. *linearis*	Synonym
NBG0263975	*Callistemon rigidus* R Br.	*Melaleuca linearis* Schrad. & J.C.Wendl. var. *linearis*	Synonym
NBG0269962	*Callistemon rigidus* R Br.	*Melaleuca linearis* Schrad. & J.C.Wendl. var. *linearis*	Synonym
NBG1457128	*Callistemon rigidus* R Br.	*Melaleuca linearis* Schrad. & J.C.Wendl. var. *linearis*	Synonym
NBG1457130	*Callistemon rigidus* R Br.	*Melaleuca linearis* Schrad. & J.C.Wendl. var. *linearis*	Synonym
NBG1457132	*Callistemon rigidus* R Br.	*Melaleuca linearis* Schrad. & J.C.Wendl. var. *linearis*	Synonym
NBG0262928	*Melaleuca* sp.	*Melaleuca linearis* Schrad. & J.C.Wendl. var. *linearis*	Specimen could be further identified
NBG0275013	*Melaleuca hypericifolia* Sm.	*Melaleuca nesophila* F.Muell.	Misidentification
NBG0275013	*Melaleuca hypericifolia* Sm.	*Melaleuca nesophila* F.Muell.	Misidentification
NBG0269923	*Callistemon pallidus* (Bonpl.) DC.	*Melaleuca paludicola* Craven	Misidentification
NBG0262488	*Melaleuca ericifolia* Sm.	*Melaleuca parvistaminea* Byrnes	Misidentification
NBG0262488	*Melaleuca ericifolia* Sm.	*Melaleuca parvistaminea* Byrnes	Misidentification
NBG0262488	*Melaleuca ericifolia* Sm.	*Melaleuca parvistaminea* Byrnes	Misidentification
NBG0262488	*Melaleuca ericifolia* Sm.	*Melaleuca parvistaminea* Byrnes	Misidentification
NBG276758	*Melaleuca ericifolia* Sm.	*Melaleuca parvistaminea* Byrnes	Misidentification
NBG0263401	*Melaleuca* sp.	*Melaleuca parvistaminea* Byrnes	Specimen could be further identified
NBG1457129	*Melaleuca* sp.	*Melaleuca parvistaminea* Byrnes	Specimen could be further identified
NBG0137407	*Melaleuca leucadendron* L.	*Melaleuca quinquenervia* (Cav.) S.T. Blake	Unresolved taxonomy: misapplied name
NBG0113762	*Melaleuca leucadendron* L.	*Melaleuca quinquenervia* (Cav.) S.T. Blake	Unresolved taxonomy: misapplied name
NBG0263565	*Callistemon* sp.	*Melaleuca rugulosa* (Schltdl. ex Link) Craven	Specimen could be further identified
NBG0263565	*Callistemon* sp.	*Melaleuca rugulosa* (Schltdl. ex Link) Craven	Specimen could be further identified
NBG0263566	*Callistemon* sp.	*Melaleuca rugulosa* (Schltdl. ex Link) Craven	Specimen could be further identified
NBG0263566	*Callistemon* sp.	*Melaleuca rugulosa* (Schltdl. ex Link)	Specimen could be further

Accession number	Label on herbarium specimen	Corrected name	Error type
		Craven	identified
NBG0263554	*Callistemon salignus* (Sm.) Colvill ex Sweet	*Melaleuca salicina* Craven	Synonym
NBG0263555	*Callistemon salignus* (Sm.) Colvill ex Sweet	*Melaleuca salicina* Craven	Synonym
NBG0263569	*Callistemon* sp.	*Melaleuca salicina* Craven	Specimen could be further identified
NBG0263570	*Callistemon* sp.	*Melaleuca salicina* Craven	Specimen could be further identified
NBG0263570	*Callistemon* sp.	*Melaleuca salicina* Craven	Specimen could be further identified
NBG1457076	*Melaleuca* sp.	*Melaleuca salicina* Craven	Specimen could be further identified
NBG1457136	*Callistemon salignus* (Sm.) Colvill ex Sweet	*Melaleuca salicina* Craven	Synonym
NBG0262931	*Callistemon salignus* (Sm.) DC	*Melaleuca* sp.	Misidentification
NBG0263567	*Callistemon* sp.	*Melaleuca styphelioides* Sm.	Specimen could be further identified
NBG0275066	*Melaleuca hypericifolia* Sm.	*Melaleuca thymifolia* Sm.	Misidentification
NBG0270663	*Callistemon rigidus* R.Br.	*Melaleuca viminalis* (Sol. ex Gaertn) Byrnes subsp. *viminalis*	Misidentification
NBG0269930	*Callistemon viminalis* (Sol. ex Gaertn) G.Don	*Melaleuca viminalis* (Sol. ex Gaertn) Byrnes subsp. *viminalis*	Synonym / specimen could be further identified
NBG0270273	*Callistemon viminalis* (Sol. ex Gaertn) G.Don	*Melaleuca viminalis* (Sol. ex Gaertn) Byrnes subsp. *viminalis*	Synonym / specimen could be further identified
NBG0270151	*Callistemon citrinus* (Curtis) Skeels	*Melaleuca viminalis* (Sol. ex Gaertn) Byrnes subsp. *viminalis*	Misidentification
NBG0269262	*Callistemon rigidus* R Br.	*Melaleuca viminalis* (Sol. ex Gaertn) Byrnes subsp. *viminalis*	Misidentification
NBG0263553	*Callistemon rigidus* R Br.	*Melaleuca linearis* Schrad. & J.C.Wendl. var. *linearis*	Synonym
NBG0262476	*Callistemon rigidus* R Br.	*Melaleuca linearis* Schrad. & J.C.Wendl. var. *linearis*	Synonym
NBG0262476	*Callistemon rigidus* R Br.	*Melaleuca linearis* Schrad. & J.C.Wendl. var. *linearis*	Synonym
NBG0262477	*Callistemon rigidus* R Br.	*Melaleuca linearis* Schrad. & J.C.Wendl. var. *linearis*	Synonym
NBG0267118	*Callistemon pallidus* (Bonpl.) DC.	*Melaleuca salicina* Craven	Misidentification
NBG0267119	*Callistemon pallidus* (Bonpl.) DC.	*Melaleuca salicina* Craven	Misidentification
NBG0262489	*Callistemon salignus* (Sm.) DC	*Melaleuca salicina* Craven	Synonym
NBG0262489	*Callistemon salignus* (Sm.) DC	*Melaleuca salicina* Craven	Synonym
NBG0262489	*Callistemon salignus* (Sm.) DC	*Melaleuca salicina* Craven	Synonym
NBG0169930	*Melaleuca decora* (Salisb) Britten	Not Myrtaceae— probably Santalaceae, further identification required	Misidentification

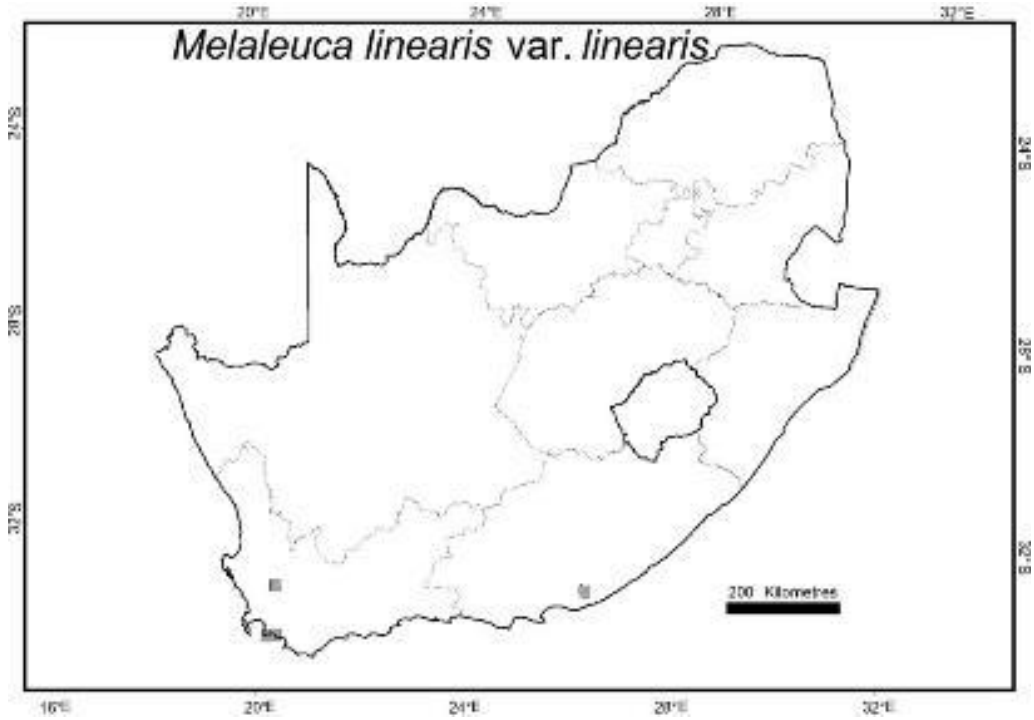
S4.2. Distribution at the quarter-degree cell scale of species of *Melaleuca* naturalized in South Africa. No map is given for *Melaleuca citrina* because historic sites of naturalization could not be confirmed or plants were no longer present.



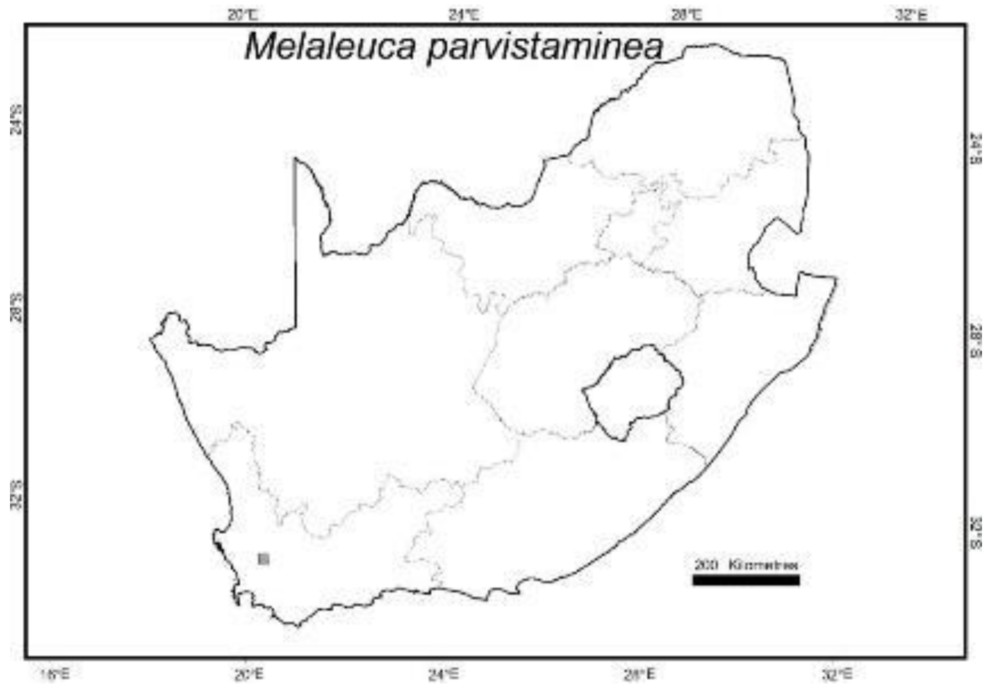
a) *Melaleuca armillaris* subsp. *armillaris.* Two known sites of naturalization



b) *Melaleuca hypericifolia*. Four known sites of naturalization

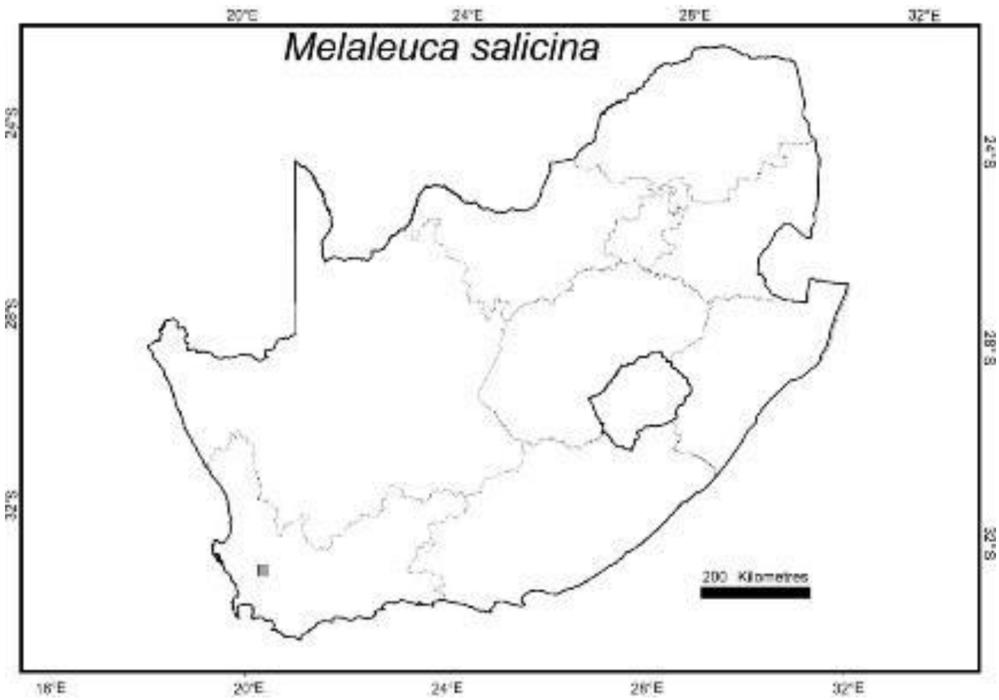


c) *Melaleuca linearis* var. *linearis*. Five known sites of naturalization

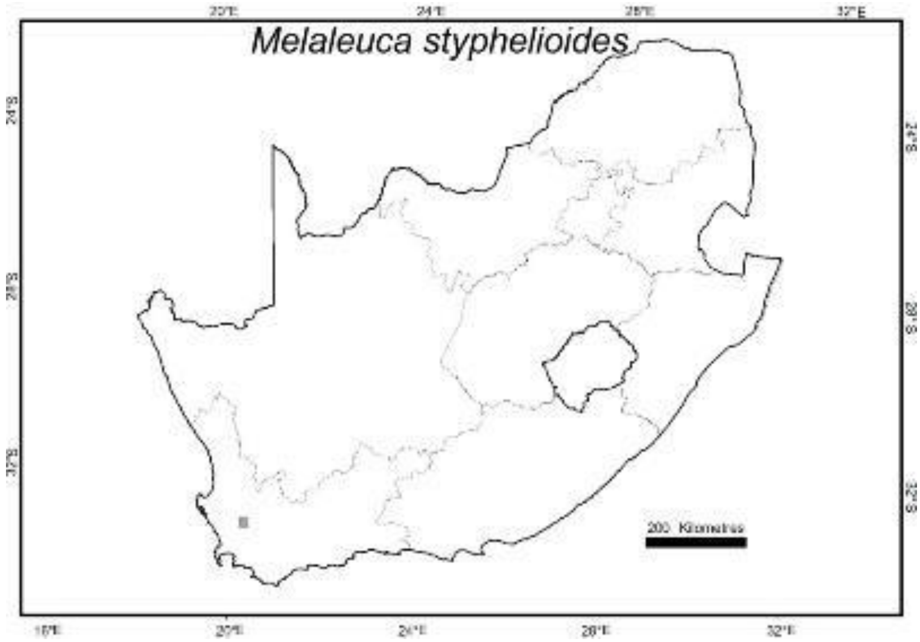


d) *Melaleuca parvistaminea*. Four known sites of naturalization

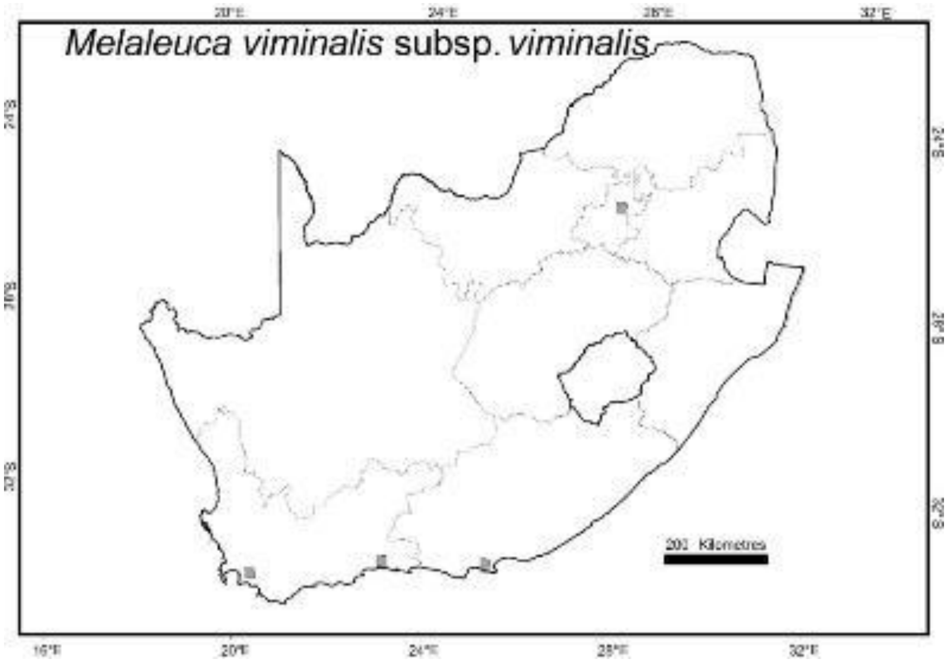
e) *Melaleuca quinquenervia*. Three known sites of naturalization.



f) *Melaleuca salicina*. One known site of naturalization



g) *Melaleuca styphelioides*. One known site of naturalization



h) *Melaleuca viminalis* subsp. *viminalis*. Four known sites of naturalization

S5.1. R code and results of generalised linear models (with binomial errors) indicating influence of traits on naturalization. Each subsequent model is improved (lower AIC) by dropping a trait which was not significant in the previous model (these are summarised in Table 5.3)

For naturalisation:

```
> mnat <- glm(as.logical(traitnoNA$NAT) ~ traitnoNA$RT + traitnoNA$HABTOT + traitnoNA$
FW +traitnoNA$MF + log(traitnoNA$HEIGHT) + log(traitnoNA$NRSCH), family=binomial)
> mnat2 <- step(mnat,test="Chi")
Start:  AIC=26.73
as.logical(traitnoNA$NAT) ~ traitnoNA$RT + traitnoNA$HABTOT +
    traitnoNA$FW + traitnoNA$MF + log(traitnoNA$HEIGHT) + log(traitnoNA$NRSCH)

                        Df Deviance    AIC     LRT   Pr(>Chi)
- traitnoNA$MF           1   12.798 24.798  0.0637  0.800746
- log(traitnoNA$NRSCH)   1   13.521 25.521  0.7870  0.375009
<none>                       12.734 26.734
- traitnoNA$HABTOT       1   19.115 31.115  6.3813  0.011533 *
- log(traitnoNA$HEIGHT)  1   19.790 31.790  7.0562  0.007899 **
- traitnoNA$FW           1   20.455 32.455  7.7212  0.005458 **
- traitnoNA$RT           1   32.122 44.122 19.3875 1.067e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step:  AIC=24.8
as.logical(traitnoNA$NAT) ~ traitnoNA$RT + traitnoNA$HABTOT +
    traitnoNA$FW + log(traitnoNA$HEIGHT) + log(traitnoNA$NRSCH)

                        Df Deviance    AIC     LRT   Pr(>Chi)
- log(traitnoNA$NRSCH)   1   14.220 24.220  1.4222  0.233041
<none>                       12.798 24.798
- traitnoNA$HABTOT       1   19.324 29.324  6.5260  0.010631 *
- traitnoNA$FW           1   20.938 30.938  8.1405  0.004329 **
- log(traitnoNA$HEIGHT)  1   21.049 31.049  8.2515  0.004072 **
- traitnoNA$RT           1   32.580 42.580 19.7824 8.678e-06 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step:  AIC=24.22
as.logical(traitnoNA$NAT) ~ traitnoNA$RT + traitnoNA$HABTOT +
    traitnoNA$FW + log(traitnoNA$HEIGHT)

                        Df Deviance    AIC     LRT   Pr(>Chi)
<none>                       14.220 24.220
- traitnoNA$HABTOT       1   19.393 27.393  5.1732  0.022938 *
- log(traitnoNA$HEIGHT)  1   21.106 29.106  6.8857  0.008689 **
- traitnoNA$FW           1   21.443 29.443  7.2227  0.007199 **
- traitnoNA$RT           1   34.702 42.702 20.4822 6.019e-06 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

For invasion:

```
> minv <- glm(traitnoNA$INV ~ traitnoNA$RT + traitnoNA$HABTOT + traitnoNA$FW +traitnoN
A$MF + log(traitnoNA$HEIGHT) + log(traitnoNA$NRSCH), family=binomial)
> minv2 <- step(minv, test="Chi")
Start:  AIC=31.49
traitnoNA$INV ~ traitnoNA$RT + traitnoNA$HABTOT + traitnoNA$FW +
    traitnoNA$MF + log(traitnoNA$HEIGHT) + log(traitnoNA$NRSCH)

                        Df Deviance    AIC    LRT Pr(>Chi)
- log(traitnoNA$NRSCH)   1   17.641 29.641 0.1538  0.69490
- traitnoNA$HABTOT       1   18.120 30.120 0.6334  0.42610
- traitnoNA$MF           1   18.490 30.490 1.0033  0.31650
<none>                       17.487 31.487
- log(traitnoNA$HEIGHT)  1   19.547 31.547 2.0606  0.15116
- traitnoNA$RT           1   21.801 33.801 4.3137  0.03781 *
- traitnoNA$FW           1   22.651 34.651 5.1642  0.02306 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Step:  AIC=29.64
traitnoNA$INV ~ traitnoNA$RT + traitnoNA$HABTOT + traitnoNA$FW +
    traitnoNA$MF + log(traitnoNA$HEIGHT)

                        Df Deviance    AIC    LRT Pr(>Chi)
- traitnoNA$HABTOT       1   18.226 28.226 0.5855  0.44418
- traitnoNA$MF           1   18.985 28.985 1.3443  0.24628
- log(traitnoNA$HEIGHT)  1   19.615 29.615 1.9744  0.15998
<none>                       17.641 29.641
- traitnoNA$FW           1   22.708 32.708 5.0669  0.02439 *
- traitnoNA$RT           1   22.748 32.748 5.1073  0.02383 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Step:  AIC=28.23
traitnoNA$INV ~ traitnoNA$RT + traitnoNA$FW + traitnoNA$MF +
    log(traitnoNA$HEIGHT)

                        Df Deviance    AIC    LRT Pr(>Chi)
- traitnoNA$MF           1   19.568 27.568 1.3421  0.24666
<none>                       18.226 28.226
- log(traitnoNA$HEIGHT)  1   21.341 29.341 3.1146  0.07759 .
- traitnoNA$RT           1   22.795 30.795 4.5690  0.03256 *
- traitnoNA$FW           1   22.886 30.886 4.6597  0.03088 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Step:  AIC=27.57
traitnoNA$INV ~ traitnoNA$RT + traitnoNA$FW + log(traitnoNA$HEIGHT)

                        Df Deviance    AIC    LRT Pr(>Chi)
<none>                       19.568 27.568
- log(traitnoNA$HEIGHT)  1   21.793 27.793 2.2245  0.13584
- traitnoNA$FW           1   23.179 29.179 3.6108  0.05740 .
- traitnoNA$RT           1   24.085 30.085 4.5166  0.03357 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```