Determinants of introduction and invasion success for Proteaceae

by

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Abstract

Successful biological invasions take place when species introduced to regions outside their natural dispersal range overcome several barriers and establish, persist, proliferate and spread potentially resulting in major threats to biodiversity. The success of invasive alien plants depends on species-specific traits and characteristics of the introduced environment. In this thesis I explore which species traits are important and which environmental barriers need to be overcome for an invasion to occur using Proteaceae as a test case. Firstly, I assessed the global introduction history and invasion ecology of Proteaceae - a large plant family with many taxa that have been widely disseminated by humans, but with few known invaders. This revealed that at least 402 species (i.e. 24% of 1674 species in this family) are known to have been moved by humans out of their native ranges, 58 species (14%) have become naturalized and 8 species (2%) are invasive. The probability of naturalization was greatest for species with large native range sizes, low susceptibility to *Phytophthora* root-rot disease, larger seeds, mammal-dispersed seeds and those with the capacity to resprout after fire or other disturbances. The probability of naturalized species becoming invasive was greater for species with larger range sizes, species used as barrier plants, taller species, species with smaller seeds, serotinous species, and those that regenerated mainly through re-seeding. Secondly, I looked at mechanisms underlying naturalization on a regional scale, using species which are not already classified as major invaders. At least 26 non-native Proteaceae species have been introduced to, and are cultivated in, South Africa. Propagule pressure facilitated the naturalization of *Hakea salicifolia* populations in climatically suitable areas, but in suboptimal climates human-mediated land disturbance and land management activities are important for naturalization. Similar drivers are important for naturalization of other alien Proteaceae: a long residence time, fire regimes, poor land management, and propagule pressure were important mechanisms for naturalization. Thirdly, I determined whether reproduction, which in part drives propagule pressure, serves as a barrier for naturalization. I examined several Australian Proteaceae species introduced to South Africa and observed that all species were heavily utilized by native nectar-feeding birds and insects. The five *Banksia* species that were assessed are self-compatible but four species have a significantly higher reproductive output when pollinators visit inflorescences. Fruit production in *H. salicifolia* does not differ between naturally-pollinated and autonomously-fertilized flowers. Moreover, no significant difference in fruit production was observed between the five pollination treatments (i.e. natural, pollen-supplementation, autonomous, hand-selfed and hand-crossed treatments) and naturalized and non-naturalized populations. However, pollen limitation was detected in non-naturalized populations which received fewer pollinator visits than naturalized populations. Thus, reproduction limits but is not a fundamental barrier to invasion for *H. salicifolia*. I conclude that reproductive success of the studied Proteaceae, which is a key barrier determining invasiveness, is not limited by autonomous seed set or mutualisms in the introduced range. In this thesis I highlight biogeographical characteristics, a set of life-history traits and ecological traits as important determinants of invasiveness. These traits are in turn dependent on the stage of invasion. Characteristics of the recipient environment are also important drivers of invasions. This study provides a better understanding of plant invasions in general, but the patterns and processes of invasions highlighted in this thesis will be particularly useful for the current and future management of alien Proteaceae in South Africa and elsewhere, as well as, other species that are adapted to Mediterranean and nutrient poor ecosystems. For example, combining traits of invasiveness and susceptible environments will help to identify which non-native species pose a high risk of becoming invasive (e.g. species with large home ranges and barrier plants) and which conditions in the target area are likely to facilitate or exacerbate invasions (e.g. strong climate match and high propagule pressure).

Abstrak

Suksesvolle biologiese indringing vind plaas wanneer ŉ spesie geïntroduseer word in ŉ area buite sy natuurlike verspreidings area, sekere versperrings oorkom, vestig, bly voortbestaan, vermenigvuldig en versprei en potensieel ŉ groot bedreiging inhou vir biodiversiteit. Die sukses van uitheemse indringer plante hang af van spesifieke kenmerke van die spesie en kenmerke van die omgewing waarin dit geïntroduseer word. In hierdie tesis maak ek gebruik van Proteaceae om te ondersoek watter kenmerke is belangrik en watter omgewing versperrings moet oorkom word vir indringing om plaas te vind. Ten eerste assesseer ek die wêreldwye introduksie geskiedenis en indringers ekologie van Proteaceae – ŉ groot plant familie wat wyd gebruik word deur mense, maar met min indringer spesies. Dit het gewys dat mense ten minste 402 spesies (dus 24% van die 1674 spesies in die familie) uit die inheemse areas verskuif het, 58 spesies (14%) genaturaliseer het en 8 spesies (2%) indringers geword het. Die moontlikheid van naturalisasie was die grootste vir spesies met ŉ groot inheemse streek, lae vatbaarheid vir *Phytophthora* wortelvrot, groter sade, dier verspreide sade en die met ŉ vermoë om weer uit te spruit na ŉ vuur of ander versteuring. Die moontlikheid van genaturaliseerde spesies om indringers te word, was groter vir spesies met groter streek grootte, spesies wat as versperring plante gebruik word, hoër spesies, spesies met kleiner sade, serotiniese spesies, en die wat hoofsaaklik voortbestaan as saadspruiters. Tweedens, het ek gekyk na onderliggende meganismes op ŉ regionale skaal, deur gebruik te maak van spesies wat nie alreeds as belangrike indringers geklassifiseer is nie. Ten minste 26 nie-inheemse Proteaceae spesies is alreeds geïntroduseer en word gekultiveer in Suid Afrika. Propaguul druk fasiliteer die naturalisering van *Hakea salicifolia* populasies in areas met geskikte klimaat, terwyl in areas met ŉ sub optimale klimaat, versteurings deur mense en grond bestuurs aktiwiteite belangrik is vir naturalisering. Die selfde drywers is belangrik vir die naturalisering van ander uitheemse Proteaceae: lang verblyftyd, vuur bestel, swak land bestuur en propaguul druk. Derdens het ek bepaal of reproduksie, wat gedeeltelik propaguul druk dryf, ŉ versperring is vir naturalisasie. Ek het gekyk na verskeie Australiese Proteaceae spesies wat geïntroduseer is in Suid Afrika, en het gevind dat al die spesies besoek word deur inheemse nektar etende voëls en insekte. Die vyf *Banksia* spesies wat geassesseer is, kan self bestuif, maar vier van die spesies het ŉ betekenisvolle hoër reproduksie wanneer bloeiwyses deur bestuiwers besoek word. Vrug produksie verskil nie tussen natuurlik bestuifde en self bestuifde blomme in *H. salicifolia* nie. Verder was daar geen verskil tussen vrug produksie van die vyf bestuiwings behandelinge (naamlik: natuurlik, stuifmeel bygevoeg, self, hand self en hand kruis) en tussen genaturaliseerde en nie genaturaliseerde populasies. Ewenwel, stuifmeel beperking is gevind in nie-genaturaliseerde populasies wat egter ook minder besoeke ontvang het dan die genaturaliseerde populasies. Dus, reproduksie kan die verspreiding beperk maar is nie ʼn fundamentele versperring vir indringing van *H. salicifolia* nie. My konklusies is dat die reproduktiewe sukses, wat andersins ʼn sleutel versperring is vir indringing, in die bestudeerde Proteaceae nie beperk word deur outonomiese saad produksie of mutualismes in die geïntroduseerde gebied nie. In hierdie tesis beklemtoon ek die biogeografiese karakters, lewens geskiedenis kenmerke en ekologiese kenmerke as belangrike bepalers van indringing. Hierdie kenmerke is op hulle beurt weer afhanklik van die stadium van indringing. Karakters van die ontvangende omgewing is ook belangrike dryfvere van indringing. Hierdie studie verbeter hoe ons plant indringing in die algemeen verstaan, maar die patrone en prosesse van indringing wat beklemtoon word in hierdie tesis sal besonder bruikbaar wees vir huidige en toekomstige bestuur van uitheemse Proteaceae in Suid Afrika en op ander plekke, asook vir ander spesies wat aangepas is tot Mediterreense en nutriënt arm ekosisteme. Byvoorbeeld, die kombinasie van kenmerke van indringing en vatbare omgewings sal help om te identifiseer watter uitheemse spesies ʼn hoë risiko inhou om ʼn indringer te word (byvoorbeeld spesies met ʼn groot streek grootte en versperring spesies) en watter kondisies in die teiken area die waarskynlikste indringing fasiliteer of vererger (byvoorbeeld sterk klimaat ooreenstemming en hoë propaguul druk).

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For further details see the acknowledgements section in chapter three and four.

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Chapter 1: Introduction

Successful biological invasions take place when species introduced to areas outside their natural dispersal range overcome several barriers and establish, persist, proliferate and spread (Blackburn *et al.* 2011; Richardson *et al.* 2000a). Biological invasions are one of the major threats to global biodiversity and this is largely attributed to the increase in global trade (Meyerson and Mooney 2007; Vitousek *et al.* 1997).

Despite the accelerating dissemination of plants globally, only a few species survive upon introduction and only a few of those species that successfully establish become invasive (Williamson and Brown 1986). This prompts one of the most fundamental questions in invasion biology – which factors drive invasions? To gain better insights on this topic, it is important to identify general attributes of invasive alien plants (IAPs). In this context, assessing which traits increase the probability of invasiveness and invasibility is crucial to improve our understanding on the causative mechanisms of plant invasions.

1.1 Invasive traits

Many studies have explored why some introduced species are more successful than others (Moles *et al.* 2008; van Kleunen and Richardson 2007). Research efforts are increasing and good progress has been made (Pyšek and Richardson 2007b), but consistent determinants of plant invasiveness remain elusive (and are probably an unrealistic aim). However, several general predictors have emerged (Kolar and Lodge 2001; Pyšek and Richardson 2007a; Rejmánek 2000). Some commonly accepted mechanisms influencing the success of IAPs include factors associated with: native range size (Pyšek *et al.* 2009); seed size (Grotkopp *et al.* 2002; Rejmánek and Richardson 1996); clonal growth (Kolar and Lodge 2001; Reichard and Hamilton 1997); a decrease in natural enemies (Colautti *et al.* 2004; Keane and Crawley 2002); and plant fitness (Barret 2011; Richardson *et al.* 2000b; van Kleunen and Johnson 2007).

Pines (genus *Pinus* L.) and Australian *Acacia* Mill. (*sensu lato*) species are model groups that have been well studied in the field of plant invasion biology. These taxa contain many species, have had a long history of introduction to many parts of the world and contain many species at different stages in the introduction-naturalization-invasion continuum (Rejmánek 1996; Rejmánek and Richardson 1996; Richardson *et al.* 2011; Simberloff *et al.* 2010).

Moreover, these taxa have yielded useful insights on traits that are important for invasiveness (Richardson 2006). Once the mechanisms of invasions are identified, effective control measures can be implemented. Although many hypotheses have been proposed (characteristics of the recipient environment; Levine and D'Antonio 1999; propagule pressure: Lockwood *et al.* 2005; species traits: Pyšek and Richardson 2007b; and climate suitability: Richardson and Thuiller 2007), it has proved difficult to obtain generalizations relating to the role of traits in plant invasions. Nevertheless, these model groups revealed important traits associated with invasiveness, and models based on these groups seem to work reasonably well for other woody plants. Exploring traits associated with the success of IAPs using other plant groups will reveal whether these traits are more broadly applicable and thus contribute useful insights on the general determinants of invasiveness.

1.2 Understanding interactions with the recipient environment

Successful invasions not only depend on species-specific traits but also on the characteristics of the introduced environment (Alpert *et al.* 2000; Richardson and Pyšek 2006). For this approach, climatic suitability (Guisan and Thuiller 2005), land use and human-mediated disturbance (Burke and Grime 1996; Vilà and Ibáñez 2011) are important drivers of invasions. Propagule pressure and residence time are also important determinants of invasion success (Lockwood *et al.* 2005; Simberloff 2009; Wilson *et al.* 2007). Propagule pressure influences a species ability to invade a new environment and determines the susceptibility of that environment (Colautti *et al.* 2006).

1.3 Proteaceae

The Angiosperm family Proteaceae Juss., provides an excellent study group for identifying determinants of species invasiveness and habitat invasibility in woody plants. Many species in the family are planted to produce cut flowers, for hedges and ornamental plants, in landscaping and for food. Consequently many species had a long history of introduction to regions outside their native ranges. Many species have special adaptations such as proteoid roots which facilitate nutrient uptake in impoverished soils and also frees them from forming mycorrhizal associations (Lambers *et al.* 2011; Leonhardt and Criley 1999; Myerscough *et al.* 2001); sclerophyllous leaves which evolved in response to infertile soils but which are also an adaptation to drought resistance (Jordan *et al.* 2005; Myerscough *et al.* 2001); and canopy-stored seeds in closed woody follicles (serotiny) which is particularly important in fire-prone environments.

Certain introduction pathways enhance the likelihood of invasive success by ensuring high propagule pressure (Wilson *et al.* 2009). Many Proteaceae species are popular in horticulture which is as an important pathway for IAPs in general (Dehnen-Schmutz *et al.* 2007; Reichard and White 2001; Richardson and Rejmánek 2011). Currently only a few Proteaceae species are known to be invasive (Richardson and Rejmánek 2011) and some others are naturalized. Because of the commercial importance of some species and in general the increasing interest in this family in horticulture, introduction pathways are increasing. Given these dynamics, important insights can be gleaned from seeking patterns, correlations and associations from a group with large numbers of introduced species over large geographical areas.

1.4 Aim and objectives

The overall aim of this study was to explore factors underpinning biological invasions in relation to the introduction-naturalization-invasion (INI) continuum, using Proteaceae as a test case. This was accomplished by; 1) identifying a general suite of factors underlying invasiveness of Proteaceae introduced globally; 2) exploring which traits facilitates the interaction between habitat characteristics (i.e. invasibility) and naturalization of Proteaceae, on a regional scale; and 3) assessing whether pollination serves as an impediment to successful reproduction in Proteaceae, on a local scale.

1.5 Chapter Synopsis

The thesis consists of three research chapters which are presented in the form of manuscripts to be submitted to scientific journals. The flow of each chapter follows the INI continuum (Figure 1). The system used, involving the use of one taxonomic group and identifying causative mechanisms across different invasion barriers, is aimed at providing an improved understanding of the full suite of drivers important for invasions in Proteaceae (and for introduced woody plant species in general) which will assist in informing management decisions.

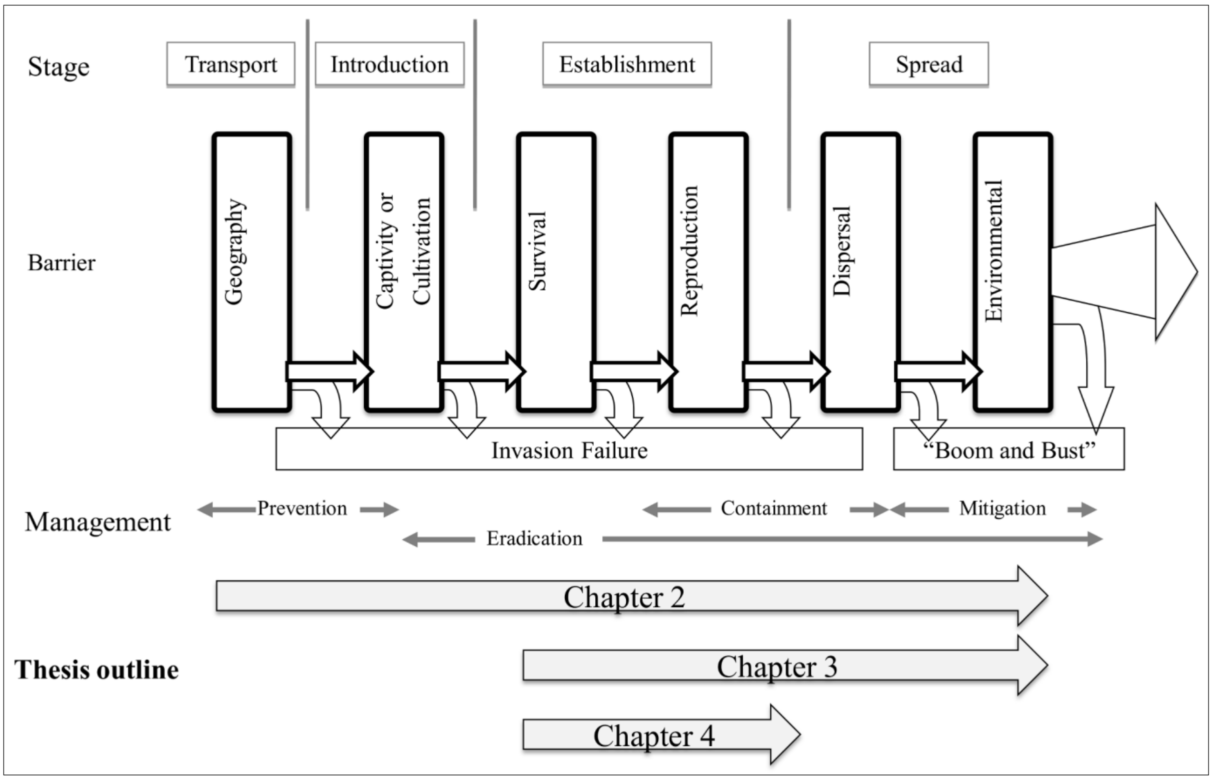

Figure 1. The introduction-naturalization-invasion (INI) continuum (adapted from Blackburn *et al.* 2011). This schematic represents barriers which alien species must overcome in order to progress across the different invasion stages. Suitable management options, which is dependent on the stage of invasion, and the structure of the thesis is also outlined.

Firstly, I compiled a global list of introduced, naturalized and invasive species and examined various traits to determine whether they were correlated with success at different stages of the INI continuum using boosted regression tree models (chapter 2).

Secondly, I collated information on localities of introduced Proteaceae species that are not already widespread invaders in South Africa. I mapped populations that have a chance to spread and examined drivers of naturalization, between naturalized and non-naturalized populations (*sensu* Pyšek *et al.* 2004). Two models were generated to explain habitat invasibility, one with all surveyed populations and one which incorporates populations in climatically suitable sites (chapter 3).

Thirdly, I focused on one barrier, reproduction, which is crucial in determining invasiveness. In this chapter I assessed reproductive fitness through breeding experiments. This is useful in determining whether reproductive performance in the introduced range is a major barrier for Proteaceae invasions (chapter 4).

Lastly, I provide a synthesis of what the results of the work presented in the three research chapters add to our knowledge of plant invasion biology (chapter 5).

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Chapter 2: Different traits determine introduction, naturalization and invasion success: Proteaceae as a test case

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JRUW: Provided comments on the manuscript and statistical advice.

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Abstract

A major aim of invasion biology is to identify characteristics of successful invaders. Many broad generalizations exist, but most meaningful associations between invasiveness and traits are context specific. Moreover, most groups tested to date (e.g. pines and acacias) have a high percentage of invasive taxa. Here we examine the global introduction history and invasion ecology of Proteaceae - a large plant family with many taxa that have been widely disseminated by humans, but with few known invaders. A global list of introduced, naturalized and invasive species was compiled. Various traits were examined to determine whether they were associated with success at different stages of the introduction-naturalization-invasion continuum using boosted regression tree models. At least 402 species of the 1674 known species in Proteaceae (24%) are known to have been moved by humans out of their native ranges, 58 species (14%) have become naturalized and 8 species (2%) are invasive. The probability of naturalization was greatest for species with large native range sizes, low susceptibility to *Phytophthora* root-rot fungus, those which have larger mammal-dispersed seeds, and those which have the capacity to resprout. The probability of naturalized species becoming invasive was greatest for species with larger native ranges, those used as barrier plants, taller species, species with smaller seeds, and serotinous species that regenerate mainly by reseeding. Therefore, some variables are positively associated with success for both naturalization and invasion, whereas others seem to play a role at only one stage, and a few have different types of influence (positive/negative) at different stages of the introduction-naturalization-invasion continuum. On their own, these observations provide little predictive power for risk assessment, but when the causative mechanisms are understood (e.g. *Phytophthora* susceptibility) they provide valuable insights. Traits driving invasiveness of Proteaceae has proved to be similar to invasive traits of pines and acacias. Therefore, we need to continue looking at different taxonomic groups to develop robust generalizations of the determinants of plant invasions. Linking the observed tendency for selecting particular traits to mechanisms will likely produce both interesting theoretical observations and management recommendations.

2.1 Introduction

Species introduced to areas outside their natural dispersal range need to overcome various barriers to establish, persist, proliferate and spread [1,2]. Some invasive species present a major threat to global biodiversity [3], therefore, it is important to understand the full suite of drivers of invasion to mitigate species impacts and prioritize management efforts. Many studies have examined invasive traits of introduced species [4,5,6,7,8]. A common approach is to seek associations between particular traits and the position of species along the introduction-naturalization-invasion (INI) continuum and to link these with underlying mechanisms [9,10,11,12,13,14]. These types of studies are important because introduced species are influenced by different factors at each stage of the INI continuum and these interacting factors and processes determine the fate of introduced species [2,15].

Identifying traits correlated to invasiveness is a central goal in invasion ecology, the success of which has direct application for the prediction and prevention of future invasions [16]. Although consistent determinants of plant invasiveness are elusive, several general predictors have emerged [5,8,17]. To ensure effective prevention measures of alien invaders, identifying traits correlated to invasiveness is a central goal in invasion ecology Traits associated with invasiveness include a shorter juvenile period, short reproduction intervals, small seed mass and large native range size, and this has been shown to be very important across a large number of plant taxa [12,18,19]. But taxonomic groups vary markedly in the proportion that are invasive and few taxa have been systematically studied with respect to invasive traits [20].

Among woody plants, pines (genus *Pinus* L.) and Australian *Acacia* Mill. (*sensu lato*) species have been proposed as model groups. These taxa contain many species, have a long history of introduction to many parts of the world and contain many species at different stages in the INI continuum [7,18,21,22]. Proteaceae provides an excellent alternative group for identifying determinants of invasiveness in woody plants, since, unlike *Pinus* and Australian *Acacia* species, the primary reason for introduction are for flower production or in horticulture, but many species have still had a long history of introduction to new regions [23]. Furthermore, there are relatively few invaders, despite the large number of introduced species.

Proteaceae is a large family of flowering plants occurring predominantly in the Southern Hemisphere with its greatest diversity in Australia and southern Africa [24,25,26]. The family is typically associated with nutrient-poor soils and many species have adaptations for surviving in these conditions, such as proteoid roots [27,28]. Plants with proteoid roots are advantageous because they do not rely on the presence of mycorrhiza (e.g. Pines) and root nodule bacteria (e.g. Acacia) in the introduced region [29] and thus overcome survival barriers. Another important life-history characteristic are the closed woody follicles which protect the canopy stored seeds from fire (i.e. serotiny), which are mainly released in the post-fire, low competition environment [30].

The horticultural trade is an important introduction pathway for invasive alien plants [31,32,33]. Many alien plants are introduced intentionally for specific purposes [34,35], similarly so for Proteaceae. Many Proteaceae species have attractive inflorescences, making them popular in the ornamental plant trade and leading to introductions of many species to many parts of the world. *Banksia* L.f., *Leucadendron* R.Br., *Leucospermum* R.Br. and *Protea* L. are the main genera used for floriculture and other genera such as *Aulax* Berg., *Grevillea* R.Br. ex Knight, *Isopogon* R.Br. ex Knight, *Mimetes* Salisb., *Paranomus* Salisb., *Serruria* Salisb. and *Telopea* R.Br. are used to a lesser extent [36]. In addition to ornamental uses, species in *Grevillea*, *Hakea* Schrad. & J.C.Wendl., and *Macadamia* F.Muell. are grown for food production, as barrier plants or windbreaks, and landscape plants. Given that many species are used in the horticultural trade, which is an important invasion pathway for other plant families, a number of introduced species are expected to be invasive [31,32, the tens rule; 37].

Some groups comprise many invaders, such as *Pinus* and Australian *Acacia* species [33], and others less so [20,38], such as *Piper* L. and *Rhododendron* L. [33]. Some Proteaceae are major invaders, including *Hakea drupacea*, *H. gibbosa*, *H. sericea* [39] and *Grevillea robusta* (PIER, http://www.hear.org/pier/), but there are fewer invasive species in this group than other widely introduced taxa. However, because of the commercial importance of some species and the increasing interest for Proteaceae in horticulture [40], there have been more introductions recently.

In this study, we aim to identify a general suite of factors underlying invasion success in a non-model group. Specifically, we assessed:

1) which Proteaceae have been introduced worldwide;
2) the invasion status of all introduced species;
3) whether certain genera are favoured at any stage of invasion; and
4) which traits facilitate the transition from introduction to naturalization and naturalization to invasion.

2.2 Methods

2.2.1 Global Proteaceae Inventory

We developed a global list of Proteaceae species from many sources (Table S1). Synonyms were taken into account during searches and name changes were documented (See Table S2 for more details). In terms of genera, Weston and Barker [24] classified 80 genera comprising 1702 species and Mabberley [41] recorded 1775 species belonging to 75 genera. We based the number of genera in this family according to the list compiled by Weston and Barker [24], updated with a couple of recent changes, e.g. the merger of *Banksia* and *Dryandra* [42; see Table S2 for reference to the species list].

2.2.2 Status as introduced species

We conducted extensive surveys of databases, floras, published sources and corresponded with experts (for lists of sources consulted see Table S1) to develop lists of species at different points along the INI continuum. Species were recorded as introduced if they were found to occur in a biogeographical region outside their native range. Species were only recorded as naturalized or invasive [*sensu* 43] if this was clearly mentioned in the literature or when this could be established through communication with experts. Naturalized species form self-replacing populations, while invasive species form self-replacing populations at a considerable distance from the parent plant and has the potential to spread over long distances (i.e. more than one hundred metres in less than fifty years for taxa spreading by propagules).

2.2.3 Phylogenetic patterns

To assess how human-mediated dispersal facilitates invasiveness across different genera of Proteaceae, we performed three hierarchical comparisons: 1) species not known to be introduced vs. introduced species; 2) introduced (but not naturalized) species vs. naturalized species; and 3) introduced (but not invasive) species vs. invasive species. The random expectation was generated using the hypergeometric distribution [44]. This taxonomic level approach tests whether the numbers of introduced, naturalized and invasive species are non-random by comparing the proportion of introduced, naturalized and invasive species with the total number of species in the Proteaceae family. Genera falling between the 95% confidence intervals were considered similar to that of a random expectation. Genera above or below the intervals were significantly over- or underrepresented respectively.

2.2.4 Selection of traits

We included traits in the database that have been shown to be useful for separating invasive from non-invasive species in previous comparative studies (Table 1; see Table S3 for reference sources used for traits). These included vegetative, ecological, and reproductive traits and features of the distribution of taxa. In addition, because Proteaceae species are mainly introduced for horticulture, we assessed whether features linked to the demand for different species in horticulture are important for promoting the likelihood of introduction. Three specific traits were used as putative indicators of horticultural demand: inflorescence size, bloom colour and use (i.e. purpose for species introductions). Trait data were collected for as many species as possible. However, this was dependent on the availablility of data which is often not readily available for non-introduced species.

2.2.5 Analysis of traits important at various stages

We used boosted regression trees (BRT) to explore the relationship between the explanatory and response variables. This is a machine learning approach where the final model is not predetermined but learned from the data. This method makes use of two powerful techniques, boosting and regression trees [45]. The boosting component of this method increases the predictive performance of the model and reduces over fitting which allows for more robust estimates [45]. We assessed factors important at each stage in the invasion process to determine the relative influence of the explanatory variables and the amount of variance explained by the model. All analyses were carried out in R (version 2.15.1, R Development Core Team, 2012) using the gbm package for BRT [46].

Before constructing the BRT models we tested for co-linearity between the predictor variables using the Kendall rank correlation coefficient. There was no strong correlation in the data between any two variables (max r^2=0.64), therefore we included all variables in the analyses (Figure S1). BRT models were fitted with Bernoulli error distributions since the response variables are binary. As trait data was not available for all species with a possible bias between introduced species and the likelihood of trait data having been recorded, we restricted the comparisons to introduced (but not yet naturalized) vs. naturalized; and naturalized (but not invasive) vs. invasive.

For each stage, we selected the optimum model settings based on recent guidelines [45]. We specifically aimed to achieve a model with at least 1000 trees with minimum predictive deviance [45]. Height, seed mass and range size were log transformed for the analyses. The fitted BRT naturalization and invasion models comprised the following parameter settings; a two-way interaction model (tree complexity=2) with a slow learning rate of 0.0005 and a bag fraction of 0.5. Tree complexity limits the number of nodes allowed for each tree in the boosting sequence to main effects only (tree complexity=1) or interaction of variables (e.g. tree complexity=2); the learning rate specifies the weight of each successive tree added to the prediction model; and the bag fraction parameter specifies the proportion of data selected at each iteration which improves predictive performance [45]. The final models comprised an optimal number of 2600 trees for the naturalization model, while the loss function was minimized at 5500 trees for the invasion model.

Initially, we performed the analysis using the full dataset comprising 14 predictor variables (Table 1). The model showed native range size to be one of the important variables determining naturalization (Figure S2). Since most of the naturalized species and all invasive species are from Australia, and native range sizes differed for the different bio-geographic regions, we decided to restrict the rest of the analysis to Australian taxa (Table S5). This also allowed the inclusion of the range sizes of non-introduced species as almost all Australian taxa have such data. To test the importance of range size along the INI continuum we used independent Mann-Whitney Wilcoxon tests.

2.3 Results

At least 402 species (24%) out of the 1674 species recognized here have been introduced outside their native ranges (Figure 1; Table S4). Introduced species that have not yet naturalized include 336 species (84%), 58 species (14%) are considered naturalized, but not invasive and 8 species (2%) are invasive. Australia is home to 1121 Proteaceae species and at least 206 species (18%) have been recorded as introduced worldwide (Figure 1; Table S4). We recorded 147 Australian species (71%) that have been introduced out of their native range but which have not yet naturalized, 51 naturalized species (25%) which are not yet invasive, and 8 invasive species (4%). All invasive species and ~90% of naturalized species are native to Australia.

Of the 79 Proteaceae genera, most have a similar number of naturalized or invasive species to that expected from a random distribution (Figure 2), but eight genera are over-represented and seven are poorly represented from the introduced Proteaceae (Figure 2a). Moreover, 29 genera contain species which have naturalized, with three Australian genera (*Macadamia*, *Hakea* and *Grevillea*) overrepresented on the lists and three South African genera (*Leucadendron*, *Leucospermum* and *Protea*) under-represented (Figure 2b). *Hakea* is over-represented in terms of invaders (Figure 2c).

2.3.1 Transition from introduction to naturalization for Australian Proteaceae

The BRT naturalization model accounted for 12% of the mean total deviance (1-mean residual deviance/mean total deviance). Boosted regression tree models generate an index of relative influence of all variables, this is calculated by summing the contribution of each variable. The six most influential variables predicting naturalization of Australian species are native range size, dispersal vectors, susceptibility to *Phytophthora*, fire survival mechanisms, seed mass and the number of flowering months (Table 2; Figure S2).

2.3.2 Transition from naturalization to invasion for Australian Proteaceae

The BRT invasion model accounted for 36% of the mean total deviance. Barrier plants, plant height, native range size, seed mass, serotiny and fire survival mechanisms comprised the six most influential variables predicting invasion (Table 2; Figure S3).

2.3.3 Influential variables predicted from the BRT models

The source pool of 1121 Australian species encompasses a large geographic distribution. Native range size differed significantly across stages in the invasion continuum (Figure 3). Introduced species occupied larger home range sizes than non-introduced species (W = 55874, $p < 0.05$, 95%CI = -59378 to -30957), naturalized species occupied larger ranges than the pool of introduced species (W = 2954, $p < 0.001$, 95%CI = -146446 to -25971), but invasive species did not differ in range size when compared to naturalized species (W = 136, p = 0.13, 95%CI = -370985 to 61624). On average, invasive species inhabit larger ranges (447688 km^2 ± 136193, mean ± SE) than introduced but not naturalized (211890 km^2 ± 40457) and naturalized but not invasive (318092 km^2 ± 55782) species.

Several other variables were important. The level of *Phytophthora* susceptibility prominently influences naturalization and invasion success (Figure 4). Only a few susceptible species managed to survive and establish but only resistant species progressed to become invasive (Figure S2 & S3).

Species response to fire differed between the stages of invasion (Figure 5). Resprouters were more likely to become naturalized (Figure S2) but re-seeders successfully invaded (Figure S3). Moreover, serotiny is an adaptation to fire and serotinous species had a greater chance of becoming invasive (Figure S3).

Seed mass was an important predictor of naturalization and invasion, but in contrasting ways. For naturalization large seeds (34.48g ± 5.79) are important (Figure S2). Conversely, small seeded plants (23.21g ± 3.47) are more likely to invade (Figure S3). Dispersal vectors are important for naturalization. Species dispersed by mammals are more likely to naturalize and wind dispersal also comprises an important vector for a large proportion of species (Figure S2; Table S6).

Species that flowered for longer periods had a higher probability of successfully naturalizing (Figure S2). The length of a long flowering period varied from four months to all year round.

Australian Proteaceae species have been introduced worldwide for many uses but the pool of introduced species mainly comprised species used as barrier plants and for ornamental purposes (Table S4). Many introduced species have a combination of uses. For example, *Banksia ericifolia* is used for ornamental purposes, as a barrier plant and for cut flowers. The BRT invasion model predicted the use of barrier plants to be the most important trait conferring invasiveness (Table 3; Figure S3).

Finally plant height is an important correlate of invasiveness for Proteaceae, with taller species having a significantly (W = 108, p = 0.03) higher tendency to become invasive (Figure 6).

2.4 Discussion

2.4.1 General patterns of invasiveness

Within Proteaceae, species that are useful to humans have been introduced more often. This finding is not surprising since humans prefer species that are attractive or beneficial [31,47]. Once the introduction barrier was overcome, several variables were important for naturalization and invasion. The probability of naturalization is greatest for species with large range sizes, low susceptibility to *Phytophthora* and larger seeds. Species that are wind dispersed and resprout are also likely to naturalize. The likelihood of a naturalized species becoming invasive was associated with species that are used as barriers or wind breaks, tall in stature, large home ranges, are small-seeded, serotinous and re-seeds after a fire.

An initial filter to biological invasions involves plants overcoming introduction barriers. Human-mediated pathways are responsible for introducing alien species into novel areas and therefore play an essential role as dispersal vectors [48]. Understanding the introduction history of Proteaceae is an essential step towards improving our understanding of plant invasions because of the strong correlation between introduction pathways and invasion success [49]. Several Proteaceae genera from Australia, South Africa and New Caledonia have many more introduced species than expected from a random distribution (Figure 2a). These genera were largely introduced for cut-flowers and ornamental uses (Table S4). Humans are thus largely responsible for intentional Proteaceae introductions and there is a preference for species that are considered attractive. Although a few South African genera are introduced more than expected, unlike the Australian genera, these genera do not conform to our naturalization expectation (Figure 2b). For Australian genera, *Hakea* have more naturalized and invasive species than expected by chance (Figure 2b & 2c). The *Hakea* genus includes high-risk species, particularly in South Africa. In South Africa, *Hakea* species are among the most aggressive invaders in fynbos where they form monospecific stands over large areas [50,51]. Although there are relatively few invasive species in this group at present, human preference for certain species indicates taxonomic bias and this may potentially influence trait related patterns.

The effect of native range size is similar to that seen in many other taxonomic groups. Proteaceae species with large native ranges are more likely to naturalize and overcome barriers. This is consistent with studies examining geographic distribution as a trait conferring invasiveness [12,52]. There are a few potential explanations for this. Firstly, humans are more likely to encounter widespread species and introduce them elsewhere [53]. Secondly, wide-ranging species are tolerant of a wider range of environmental conditions which increases their probability of establishment in a new area [53]. Lastly, species occupying larger ranges can be matched to suitable climates prior to introduction to ensure successful establishment. Large native geographical distributions can therefore be considered an important factor that pre-adapts a species for successful invasion.

The mechanistic relationship between correlates of invasiveness is not always apparent. But for Proteaceae, susceptibility to *Phytophthora* is clearly an important trait with predictive power for risk assessments. A number of *Phytophthora* species are known to affect Proteaceae, the most common being *Phytophthora cinnamomi* and *P. nicotianae* [54]. Diseases caused by these pathogenic species, of which root-rot is most common, are destructive since it usually results in rapid and sudden death of the infected plant [54]. Given that these pathogens cover a wide distribution, resistance to these species will favour establishment success [55]. Here we showed species that were less susceptible to the fungus had a greater chance of becoming naturalized but only species showing resistance progressed along the continuum to successful invasion. *Phytophthora* resistance plays a big role in limiting invasions because none of the susceptible species progressed through the invasion barriers. Moreover, naturalization into *Phytophthora* free areas may be possible, but invasion requires *Phytophthora* resistance. The level of susceptibility to this pathogen is, therefore, a major limiting factor of naturalization and invasion in this group.

Vegetative reproduction has been shown to be a common predictor of invasiveness [5,56,57]. We found that species which reproduced by resprouting have high potential for naturalization. But re-seeding alien species have a greater chance of becoming invasive since seven of the eight invasive species possess this strategy (Figure 5). Proteaceae tend to occur in fire prone environments. An investment in producing seeds rather than allocating resources to vegetative reproduction will be more advantageous in environments with short fire-return intervals, such as in fynbos. Fire regimes potentially explains why introduced South African

Proteaceae (83% are reseeding species; Table S4) fail to invade Australian ecosystems (i.e. long fire-return intervals delay recruitment) but introduced Australian serotinous species are successful in South African fynbos (i.e. short fire-return intervals provide favourable conditions for recruitment and dispersal of serotinous species). Resprouting plants allocate resources into coppicing and thus less into fruit production. This mechanism has two effects: firstly, obligate reseeders produce higher seed loads which increases propagule pressure and thus increases the likelihood of invasion; secondly plants that resprout may have the same invasive potential but because of their smaller propagule pressure they will take much longer to invade and at a lower dispersal rate, but they will be more persistent [58]. Therefore, the observed trend could merely be an artefact of recent introductions (i.e. resprouters require more time to progress along the INI barriers). Given sufficient time, resprouting species may be just as capable of invading as reseeding species. Serotiny also influences the probability of naturalization. This mechanism has the advantage of not requiring a host to disperse seeds. Serotinous species therefore overcome the barriers of finding a compatible seed disperser in the new range. As a result, regeneration through seeds and canopy-stored seeds comprise ideal mechanisms driving invasions when recruitment events are favourable [58]. On the other hand, species which reproduce vegetatively are ideal for cut flowers and hedges because they are tolerant to heavy harvesting. But these species yield low fruit production and thus low propagule pressure and is therefore only recognized as important for naturalization in Proteaceae and not spread.

Another important determinant of invasiveness is seed size [18,59]. However, we found contrasting results between the two stages. Large seeded species had a higher chance of becoming naturalized, whereas small seeded plants were more likely to invade. This may be attributed to large seeds having larger nutrient reserves which favours establishment. For invasions, small seeded species are more likely to become invasive. Proteaceae are predominantly wind dispersed (Table S4), therefore small seed size is favourable. Moreover, species with small seeds can produce large numbers of seeds that can disperse further and thus have higher numbers of seeds germinating [60]. These findings are similar to other plant groups where large seed size promotes the growth of introduced species and small seed size favours successful invasions [9,61]. In order to become invasive, naturalized species must overcome dispersal barriers [2]. We also found that introduced Proteaceae are largely wind dispersed and this vector was an important determinant in the naturalization model.

Consequently, small seeds have a greater chance of spread through wind which assists in long distance dispersal [62].

Although naturalization preceeds invasion we found that the type of reproduction and seed mass demonstrated contrasting results for naturalization and invasion. Species with large seeds and a resprouting strategy had a greater probability of naturalizing, while species with small seeds and a re-seeding strategy had a greater probability of invading. The rate of spread can potentially explain this pattern. If a small seeded species which reproduces through seeds can naturalize then it is likely that this species will spread quickly, however a resprouting species with larger seeds will spread at a slower rate. Therefore, while a large seed mass and a resprouting strategy favours naturalization this results in slow spread rates and a slow transition from naturalization to invasion.

Flowering phenology, the use of barrier plants and height were important predictors of successful invasions. The length of the flowering season is also an important predictor of invasiveness in other taxa [56,57]. Proteaceae species that flowered for longer had a greater chance of naturalizing. This may be due to increasing the chance of cross pollination which ensures successful reproduction [57]. Barrier plants were more likely to become invasive; this could be attributed to the role of fires. If fire-adapted species are exposed to fires, they will have the opportunity to spread. In contrast plants in gardens and orchards are protected from fires and do not get a chance to recruit and spread. Moreover, introduced Proteaceae species used as barriers or hedges are typically planted on the edge of farms or homesteads and in some cases adjacent to natural vegetation. These land use practices often increase the risk of spread [63]. The practice of interplanting species in natural veld will also promote invasion. By contrast, plants established in orchards are out of sync with natural disturbance and recruitment cues in the adjacent veld, and rarely have a chance to invade, except following disastrous fires that move through orchards.

In many studies plant height has been shown to be correlated with invasiveness [8]. We also found that a taller stature is a potential driver of invasiveness. This could be associated with seed dispersal, where taller plants can potentially produce more seeds and disperse their seeds further.

There are already a few serious invaders in the Proteaceae group, but with many other species having been widely planted recently there are potentially many more major invaders “waiting in the wings”, for example species in the genus *Banksia* (S. Geerts et al. unpublished data). *Banksia* species were predicted to be high risk introductions in South Africa [64], specifically *B. ericifolia* was classified as a potentially invasive species in fynbos [65]. Currently, this species is invasive in at least one site (S. Geerts et al. unpublished data; Protea Atlas Project data). These studies demonstrate the value of conducting trait based assessments within this group. Moreover, Proteaceae highlights the need to do such analyses based on restricting studies to particular groups, since more focussed analyses, within particular taxonomic groups, are more likely to yield useful insights. This has also been shown in a study on Iridaceae [66].

2.4.2 Future trends for the Proteaceae industry

It is important to assess introduction pathways proactively to anticipate future species invasions. One pathway that has high demand is horticulture. Flower-producers look to produce a range of interesting and exciting products of uniformly good quality. Therefore, there is a big pressure to improve cultivars, and growers can be quite selective. Desirable plant characteristics include: increased disease resistance, longer vase life, no leaf blackening, brighter colours and better travelling qualities for cut blooms [36,67]. This is often difficult to achieve because of susceptibility to *Phytophthora*, bird and insect damage to flowers, airfreight and shipping problems which poses a risk to the quality of flowers [40; pers. com.]. There are simply too few species that meet all the demands of flower growers, nurserymen, florists and home gardeners (pers. comm. with flower growers in the Western Cape). Therefore, we suspect that “true” species will not be imported on a large scale and future expansion will in all likelihood favour the development of new hybrids. The way forward for the industry is presumably defined through breeding programs which develop cultivars with desirable characteristics. This potentially suggests that the number of invasive species in this group, with regard to “true species”, will not boom in the future. However, intentionally introduced hybrids are selectively chosen for characteristics that often confer invasiveness [68,69]. Risk assessment studies on hybrids will be a necessary step to prevent further invasions within this group.

2.5 Conclusion

The traits correlated with Proteaceae introductions and invasion highlight intriguing similarities as well as differences between invasion stages. On their own, these observations provide little predictive power for risk assessment, but when the causative mechanism is understood this provides valuable management insights. For example, *Phythopthora* susceptibility is a major barrier limiting invasions in the group. Linking the observed tendency for selecting particular traits to mechanisms will likely produce both interesting theoretical observations and management recommendations. We need to continue looking at different groups to develop robust generalizations in invasion biology. Additionally, for a better understanding of biological invasions it is not only important to identify traits of invasiveness, it is also important to ask what characteristics of the recipient environment influences invasions [70].

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Tables

Table 1. Description of the predictor variables, the criteria used to measure traits and data availability of species, using the full dataset and a dataset only containing species native to Australia.

Predictor variables	Methods of measuring	No. of species in the full dataset	No. of Australian species	Categories
Inflorescence size	Horticultural trait: Small inflorescences (<100mm in width or length) coded as 0 and large inflorescences (≥100mm in width or length) are coded as 1	359	200	Categorical, binary
Use	Horticultural trait: Agro-forestry, barrier plants, ornamental plants, forestry, fuel, land rehabilitation. Species used for tanning and medicinal purposes were not included in these groups, since we found no confirmation during surveys that these species were introduced specifically for these purposes	352	196	Categorical
Height (m)	Maximum height reported in literature	365 (0.1-40; 2.5)	202 (0.1-40; 3)	Continuous
Life-form	Based on whether species were reported as trees or shrubs	369	207	Categorical
Maturity	The number of years a species takes to first flowering	181 (1-9; 2)	28 (1-9; 3.5)	Continuous
Flowering duration	The number of months in a year that species are in flower (calculated from the start and end of flowering months)	366 (1-12; 4)	204 (1-12; 4)	Continuous
Survival mechanism	Species regeneration method: re-seeder coded as 1 or resprouter coded as 0.	343	187	Categorical, binary
Serotiny	Seeds retained on the plant coded as 1, non-serotinous (i.e. stored in the soil) coded as 0	357	195	Categorical, binary
Dispersal	Vector of seed dispersal: Unspecialized dispersal, wind, water, mammals, ants and birds	309	154	Categorical
Bird pollinated	Pollination primiarly by birds coded as 1, pollination by other vectors coded as 0	305	150	Categorical
Compatibility	Self-compatible coded as 1, self-incompatible coded as 0	114	39	Categorical, binary
Range size (km^2)	Total area a species occupies in its natural range calculated using minimum convex polygons	375 (2-3516000; 29190)	204 (131-3516000; 82360)	Continuous
Phytophthora	Degree of susceptibility to root rot fungus. Resistant (Res): unaffected species; susceptible (Sus): diseased plants with a lower chance of death; & very susceptible (VS): plant death	120	81	Categorical
Seed mass (g)	Seed weight reported in the database	197 (2.02-504.70; 19.34)	100 (2.74-501.80; 20.17)	Continuous

The range and median values for continuous variables are shown in parentheses.

Table 2. Summary of the boosted regression tree models for a) naturalization and b) invasion. We included all variables that contributed at least 5% to the models. The figures and tables are only inclusive of variables contributing at least 10% to the model. Data range includes the minimum and maximum values from the fitted functions and is representative of effect size.

Variable	Percentage contribution	Range	Important mechanisms between stages
a) Naturalization			
Range size	26.5	-1.30 to - 0.63	Large native range sizes (Figure 3)
Dispersal	18.4	-1.22 to - 0.89	Although wind dispersal is the most common, species that are dispersed by mammals tend to naturalize (Table S6)
Phytophthora	16.5	-1.41 to - 0.80	Less susceptible species can naturalize (Figure 4)
Survival mechanism	11.6	-1.17 to - 0.96	Species that survive fires by resprouting (Figure 5)
Seed mass	8.2	-1.18 to - 0.98	Larger seed size
Flowering duration	6.3	-1.20 to - 1.06	Flowering over longer periods
b) Invasion			
Barrier	33.4	-2.79 to - 1.42	Barriers plants (Table 3)
Height	22.1	-2.76 to - 1.62	Taller species (Figure 6)
Range size	16.1	-2.56 to - 1.92	Large native range sizes. But there is no effect in range size between the transition from naturalization to invasion (Figure 3)
Serotiny	8	-2.49 to - 2.03	Canopy stored seed banks
Seed mass	8	-2.38 to - 2.11	Small seed sizes
Survival mechanism	6.3	-2.50 to - 2.08	Regeneration from seeds

Table 3. The number of Australian species used as barrier plants and their status across the INI continuum.

Barrier plants	**Introduced, not yet naturalized**	**Naturalized, not yet invasive**	**Invasive**
Yes	29	15	7
No	118	36	1

Figure Legends

Figure 1. Schematic of the number of species progressing along INI continuum. The numbers of genera are shown in parentheses.

Figure 2. Taxonomic distribution of a) introduced, b) naturalized and c) invasive Proteaceae species worldwide. Each point represents a genus with lines indicating expectations from a hypergeometric distribution (median and 95% confidence intervals). Genera falling between the lines are not significantly over- or underrepresented. Genera above or below the intervals are significantly over- or underrepresented respectively.

Figure 3. The relationship between native range size and the number of species at different stages of the INI continuum. Significance was tested using the Mann-Whitney Wilcoxon test. The solid line shows the median, the lower and upper hinges of the box represents the lower and upper quartiles, the whiskers indicate the range of the data, and open circles are outliers in the dataset.

Figure 4. The association between Australian Proteaceae and the effect of the root rot fungus (Phytophthora) on the stages of invasion.

Figure 5. The relationship between introduced Australian species and their response to fires. The grey region represents counts of resprouters and the white region represents re-seeders.

Figure 6. The effect of height (m) on the number of species progressing along the invasion barriers. Significance between stages were tested using the Mann-Whitney Wilcoxon test.

Figure 1

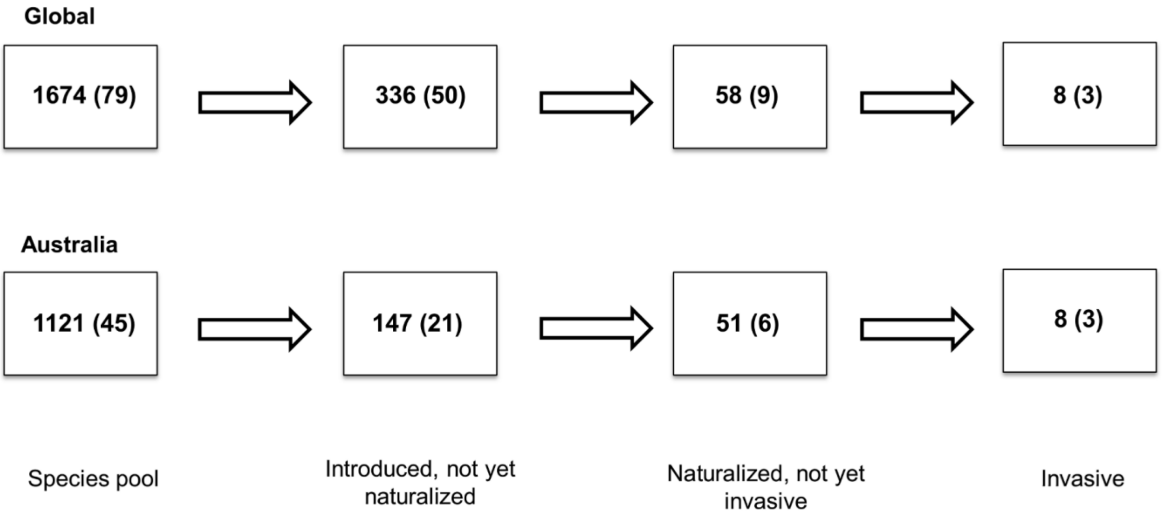
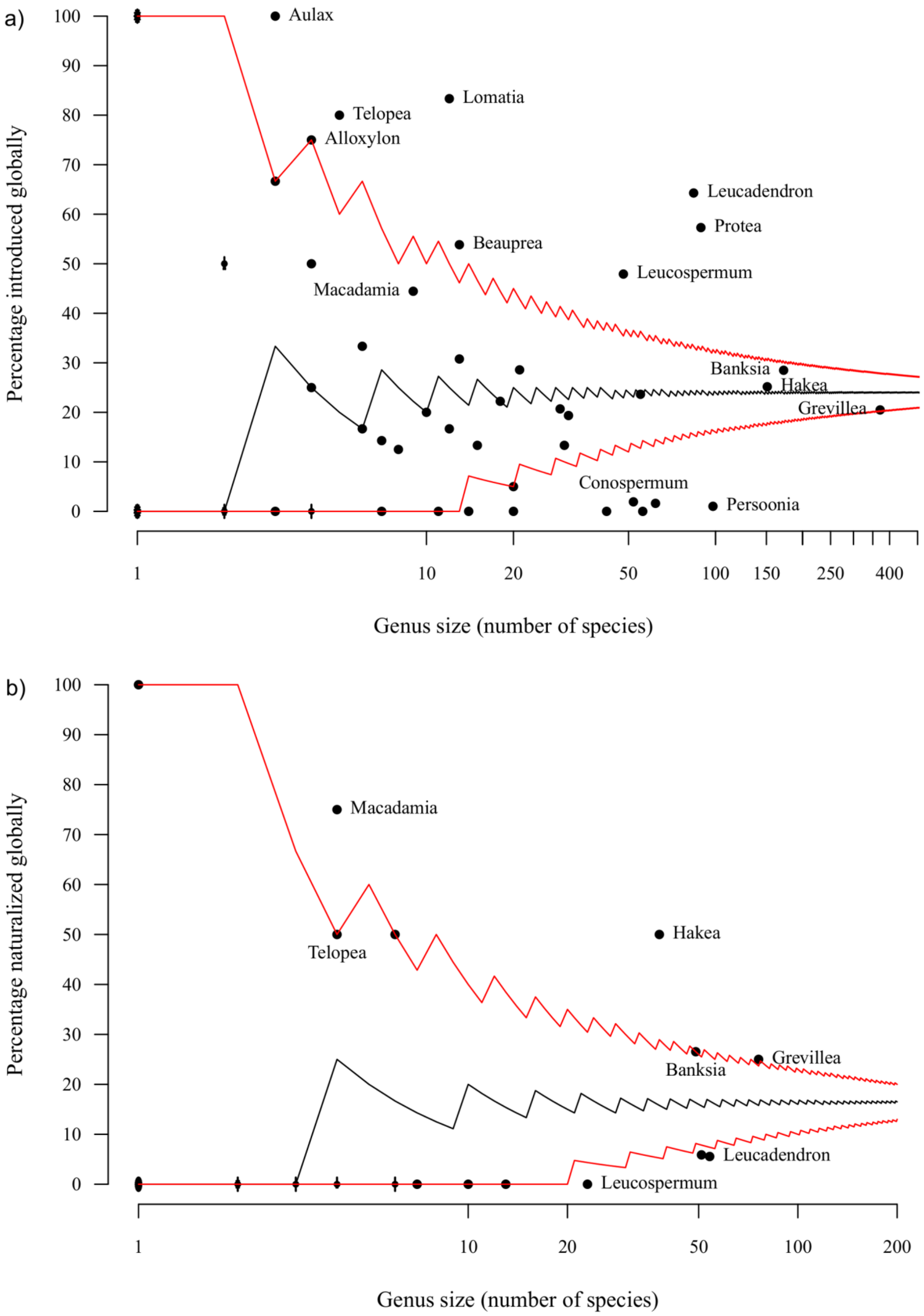

Global
1674 (79)
336 (50)
58 (9)
8 (3)
Australia
1121 (45)
147 (21)
51 (6)
8 (3)
Species pool
Introduced, not yet naturalized
Naturalized, not yet invasive
Invasive

Figure 2


a)
Percentage introduced globally
100
90
80
70
60
50
40
30
20
10
0
Aulax
Lomatia
Telopea
Alloxylon
Leucadendron
Protea
Beauprea
Leucospermum
Macadamia
Banksia
Hakea
Grevillea
Conospermum
Persoonia
1
10
20
50
100
150
250
400
Genus size (number of species)
b)
Percentage naturalized globally
100
90
80
70
60
50
40
30
20
10
0
Macadamia
Hakea
Telopea
Grevillea
Banksia
Leucadendron
Leucospermum
1
10
20
50
100
200
Genus size (number of species)

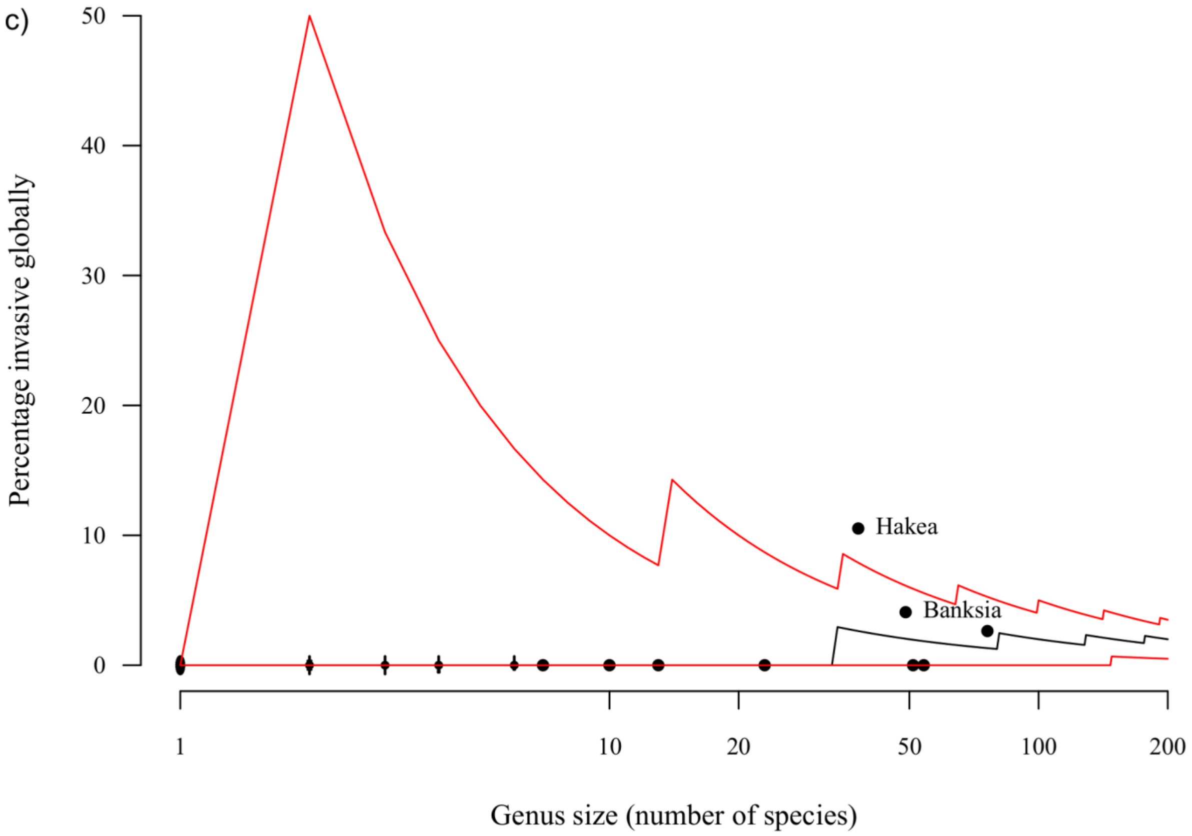

c)
Percentage invasive globally
50
40
30
20
10
0
Hakea
Banksia
1
10
20
50
100
200
Genus size (number of species)

Figure 3

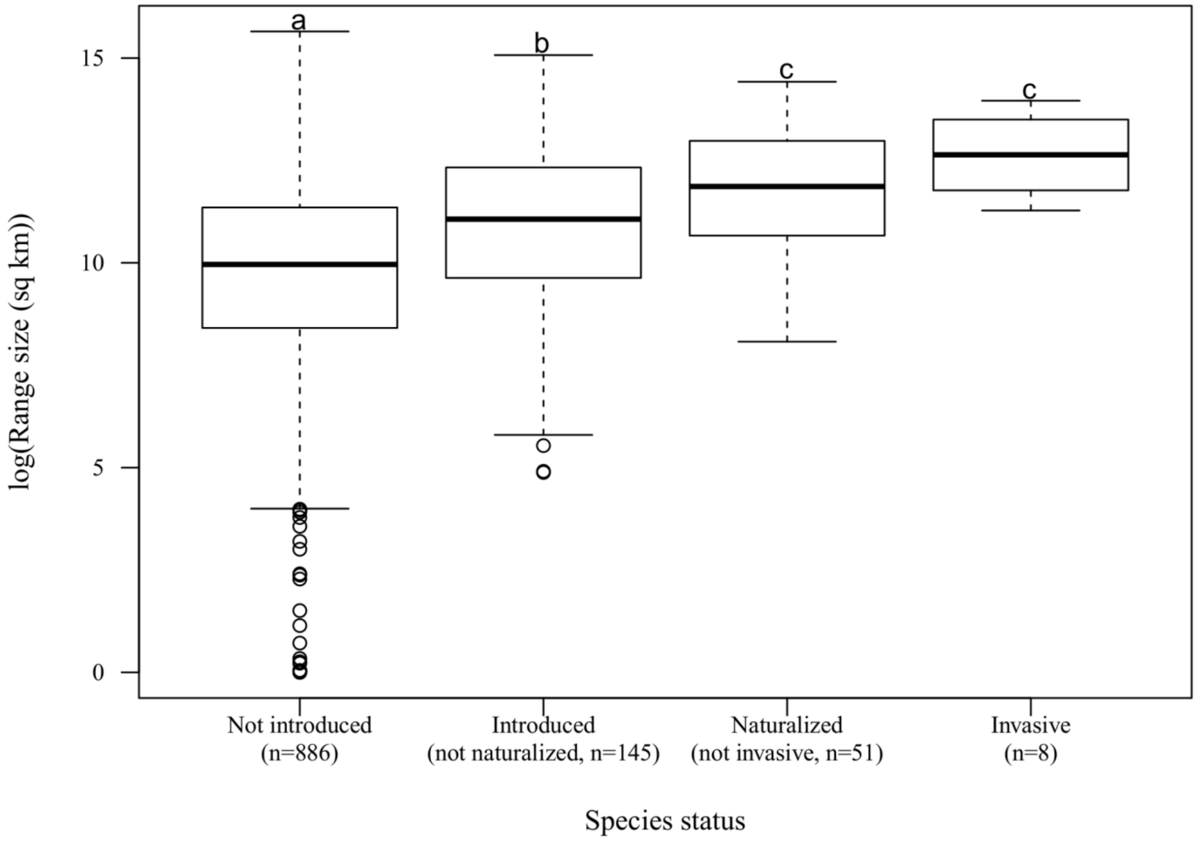

log(Range size (sq km))
15
10
5
0
a
b
c
c
Not introduced
(n=886)
Introduced
(not naturalized, n=145)
Naturalized
(not invasive, n=51)
Invasive
(n=8)
Species status

Figure 4

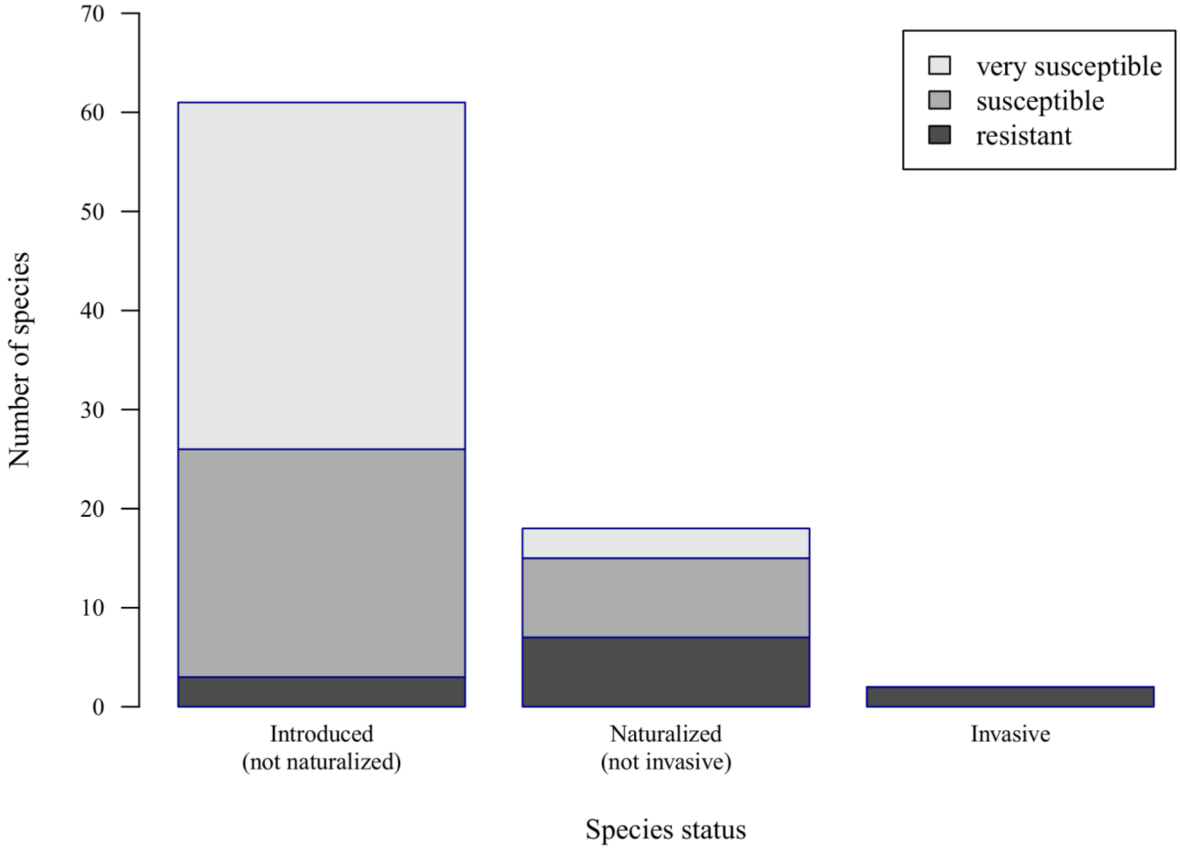
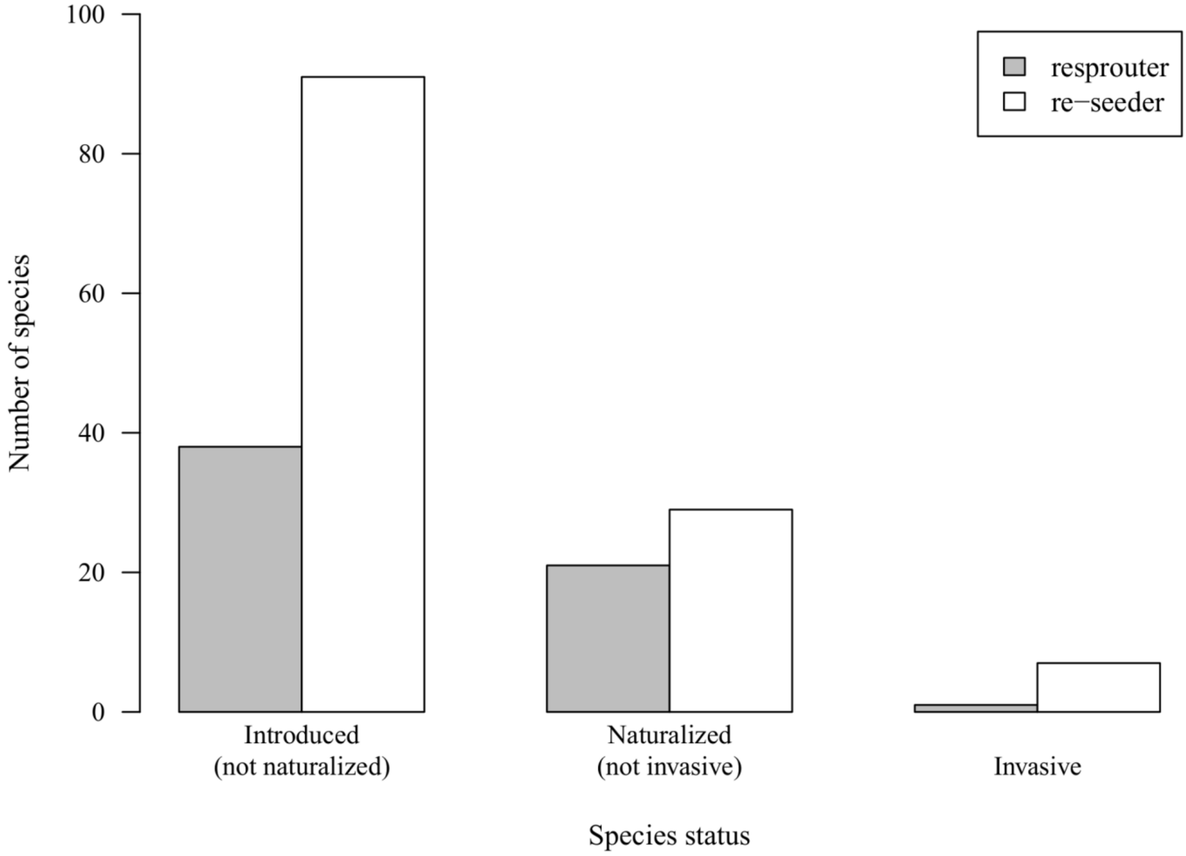
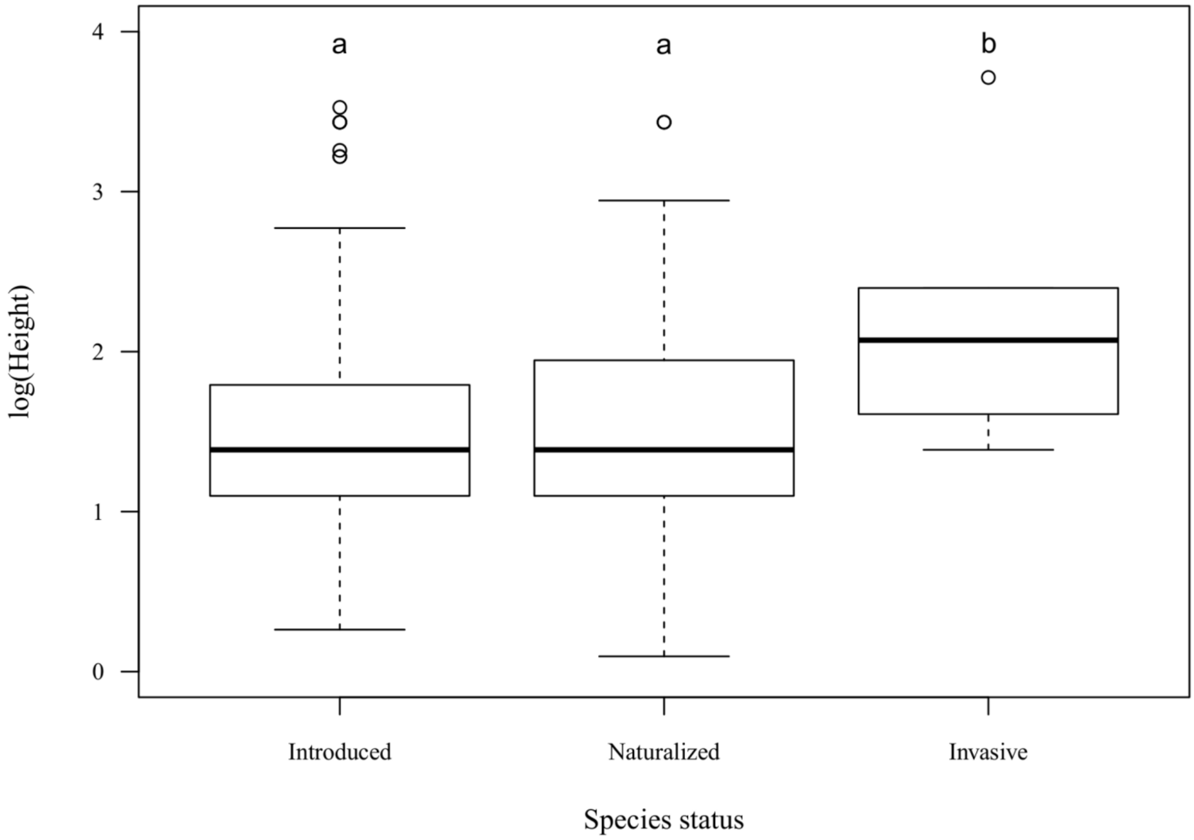

70
60
50
40
30
20
10
0
Number of species
very susceptible
susceptible
resistant
Introduced
(not naturalized)
Naturalized
(not invasive)
Invasive
Species status

Figure 5



100
80
60
40
20
0
Number of species
resprouter
re−seeder
Introduced
(not naturalized)
Naturalized
(not invasive)
Invasive
Species status

Figure 6


4
3
2
1
0
log(Height)
a
a
b
Introduced
Naturalized
Invasive
Species status

Supplementary Tables

Table S1. The furthest point along the introduction-naturalization-invasion continuum that Proteaceae species are recorded as having reached using different datasets.

	List	Usage	Numbers[1]	Description	References
Global	1.Global Compendium of weeds	Number of naturalized species	**Naturalized:** 64 (C3-E)	Database of the weedy flora of the world, based on published literature. All listed species were assumed to have naturalized (i.e. escaped from cultivation, populations are self -sustaining). These species are given the following status: weed, environmental weed, noxious weed and naturalised. No Proteaceae were listed as "invasive" in the database.	GCW published online by Rod Randall (Accessed August 2011).
	2.Global Invasive Species Database	No. of naturalized or invasive species	**Naturalized:** 1 (C3-E)	List of invasive alien species, belonging to all taxonomic groups, which pose a threat to native biodiversity. Records were obtained from a search on the family "Proteaceae". Species were not assumed to be invasive and status was based on the returned results.	GISD (Accessed June 2011).
	3.Invasive alien trees and shrubs	Number of invasive species	**Invasive:** 7 (B2-E)	Global compilation of invasive alien trees and shrubs. All Proteaceae listed were included as invasive.	Richardson and Rejmanek (2011).
	4.Global herbarium records	Number of introduced species	**Introduced:** 36 (B2-E)	All records returned from the "Proteaceae" occurrences search were downloaded. To distinguish which species were introduced to which country, the "scientific name interpreted" and "country interpreted" was cross checked with the reference list. Species lacking co-ordinates were excluded. Records of species that were introduced outside its natural range, within Australia, were included.	Global Biodiversity Information Facility (Accessed 26 August 2011)
Australia	5.Australia's Virtual Herbarium	Number of introduced species	**Introduced:** 20 (B2-E)	A search was conducted for all Proteaceae genera. If non-Australian species were present, these records were treated as introduced species. For Australian genera, each record was scrutinized for species outside its native range within Australia, except for Banksia, Hakea and Grevillea. These genera were not further examined, due to very large download files.	AVH (Accessed March 2012)
	6.The introduced flora of Australia	Number of introduced and naturalized species	**Introduced:** 207 (B2-E) **Naturalized:** 24 (C3-E)	Provides information of introduced plants grown in Australia. Information on global weedy status is provided, as well as, Australian species that have naturalized outside its native range within Australia.	R. P. Randall (2007).

South Africa	7.Southern African Plant Invaders Atlas	Number of introduced, naturalized or invasive species	**Introduced:** 13 (B1-E) **Naturalized:** 1 (C3-E) **Invasive:** 4 (B2-E)	Database providing information on the distribution, abundance and habitats of non-native plants in Southern Africa. All plants in this list were not assumed to be invasive. Species were only recorded as naturalized or invasive if this was stated in the database.	SAPIA (Accessed August 2011)
	8.Protea Atlas	Number of introduced species	**Introduced:** 18 (B2-E)	Database of species distribution in Southern Africa. It also includes ecological data of species and habitats. All alien Proteaceae were recorded as introduced. The database does indicate alien species status.	The Protea Atlas Project (Accessed August 2011).
	9.Glens cultivation list	Number of introduced species	**Introduced:** 56 (B2-E)	A listing of 34 000 plants that are cultivated in Southern Africa. All Proteaceae were recorded as introduced.	H. F. Glen (2002).
	10.Forestry trials	Number of introduced species	**Introduced:** 26 (B2-E)	A historical account of species that were introduced for forestry trials in Southern Africa. Records of location, climatic, topographic, morphological and demographic data are also provided. Grevillea was the only genus recorded.	Poynton (2009).
	11.Bolus herbarium	Number of introduced, naturalized or invasive species	**Introduced:** 5 (B2-E) **Invasive:** 1 (D1-E)	Herbarium records of alien species in South Africa. If a record was stated as invasive, then it is.	University of Cape Town, Bolus herbarium collection.
	12.Compton Herbarium	Number of introduced species	**Introduced:** 29 (B2-E)	Herbarium records of alien species in South Africa.	Kirstenbosch, Compton herbarium collection.
	13.Proteaceae flower farm (Western Cape)	Number of introduced species	**Introduced:** 15 (B2-B3)	Farmer has been exporting South African Proteaceae (flowers and cuttings) to several countries, over the past 15 years. All species that were exported for planting purposes were recorded as introduced. Hybrids were excluded.	Anonymous (pers.comm. 2012).
	14.Honingklip flower farm (Western Cape)	Number of introduced species	**Introduced:** 4 (B2-E)	Old records of plantings used for the cut flower industry.	Compton Herbarium (1989). Proteas:Nature's Pride. Protea colour prints, South Africa.
Europe	15.Flora Europaea	Number of introduced and naturalized species	**Introduced:** 2 (B2-E) **Naturalized:** 2 (C3-E)	Describes wild or widely cultivated species in Europe. Species distributions including naturalized species are provided. Proteaceae listed in this series were recorded as introduced along with their given status.	Flora Europaea (1964).

	16.European Garden Flora	Number of introduced and naturalized species	**Introduced:** 96 (B2-E) **Naturalized:** 2 (C3-E)	Cultivated ornamental plants in Europe. All plants are treated as introduced, unless classified as naturalized or invasive.	Walters *et al*. (1984-2000).
	17.Delivering Alien Invasive Species Inventories for Europe project	Number of naturalized or invasive species	**Naturalized:** 5 (C3-E)	Invasive species database for taxa in Europe. Records returned from the search for "Proteaceae" were used. Species were not assumed to be invasive and status was based on the returned results.	DAISIE (Accessed June 2011).
Hawaii	18.Breeding program	Number of introduced species	**Introduced:** 50 (B1-E)	Species, hybrids and cultivars imported to Hawaii, between 2000 and 2005, for evaluating breeding success. Successful species were released to growers. We treated all records as introduced species. Cultivars and hybrids were excluded.	Leonhardt *et al.* (2005).
	19.Cultivated plants in Hawaii	Number of introduced species	**Introduced:** 62 (B2-E)	This book gives an account of species cultivated in the Hawaiian islands. Species were only recorded as introduced, since species status was not provided.	H. St. John (1973).
Other databases	20.South India Flora	Number of introduced and naturalized species	**Introduced:** 4 (B2-E) **Naturalized:** 1 (C3-E)	Records of Proteaceae in the Palani Hills, South India. Alien species were recorded as introduced and only recorded as naturalized if this was stated.	K.M. Matthew (1999).
	21.Malesiana Flora	Number of introduced species	**Introduced:** 3 (B2-E)	Describes the flora of Malesia which spans six countries in Southeast Asia. Alien Proteaceae were only recorded as introduced, since invasion status was not given.	C. G. G. J. van Steenis (1958).
	22.Pacific Island Ecosystems at Risk	Number of naturalized or invasive species	**Invasive:** 3 (B2-E)	Records were based on a list sorted according to "Scientific names by family". Species were recorded as "naturalized" and would have been recorded as "invasive" if this was stated.	PIER (Accessed February 2012).
	23.United States Department of Agriculture (USDA)	Number of introduced, naturalized or invasive species	**Introduced:** 3 (B2-E) **Naturalized:** 2 (C3-E)	Database includes classification, distribution, threatened and endangered species and invasive and noxious weeds in the US. Species records that were returned from the "Invasive and Noxious Weeds" search were included according to their status given in the database.	The PLANTS Database (Accessed August 2011)
	24.New Zealand	Number of introduced and naturalized species	**Introduced:** 20 (B2-E) **Naturalized:** 11 (C3-E)	Checklist of 2436 records of New Zealand's plant taxa. Taxa were classified as casual, naturalized and eradicated. Records for all Proteaceae were included, except hybrids.	New Zealand naturalized plant checklist (2006).

25.Nursery Catalogue (Britain)	Number of introduced species	**Introduced:** 176 (B2-E)	This catalogue contains plants and cultivars introduced into Britain. Records returned from the "Protecaeae" search were included, hybrids were excluded.	Royal Horticultural Society, Plant Finder (2010).
26.Reunion Island	Number of introduced, naturalized or invasive	**Introduced:** 13 (B2-E) **Invasive:** 2 (D1-E)	Lists introduced, naturalized and invasive species. "Disappearance" records were recorded as introduced (7 species did not survive).	C. Lavergne (pers.comm. 2012).

The Food and Agriculture Organization of the United Nations (FAO) database was also surveyed. These data are not included in the analyses. After consulting experts regarding the listed "invasive" species, this source was deemed unreliable.

[1] Species classification (B1-E) is adapted from the framework proposed by Blackburn et al. (2011):

B1: Individuals transported beyond limits of native range, and in captivity or quarantine (i.e. individuals provided with conditions suitable for them, but explicit measures of containment are in place)
B2: Individuals transported beyond limits of native range, and in cultivation (i.e. individuals provided with conditions suitable for them but explicit measures to prevent dispersal are limited at best)
B3: Individuals transported beyond limits of native range, and directly released into novel environment
C0: Individuals released into the wild (i.e. outside of captivity or cultivation) in location where introduced, but incapable of surviving for a significant period
C1: Individuals surviving in the wild (i.e. outside of captivity or cultivation) in location where introduced, no reproduction
C2: Individuals surviving in the wild in location where introduced, reproduction occurring, but population not self-sustaining
C3: Individuals surviving in the wild in location where introduced, reproduction occurring, and population self-sustaining
D1: Self-sustaining population in the wild, with individuals surviving a significant distance from the original point of introduction
D2: Self-sustaining population in the wild, with individuals surviving and reproducing a significant distance from the original point of introduction
E: Fully invasive species, with individuals dispersing, surviving and reproducing at multiple sites across a greater or lesser spectrum of habitats and extent of occurrence

Table S2. A reference list of all Proteaceae species and synonyms identified in this study.

	Genus	**Species**
1	Acidonia	microcarpa
2	Adenanthos	acanthophyllus
3	Adenanthos	apiculatus
4	Adenanthos	argyreus
5	Adenanthos	cacomorphus
6	Adenanthos	cuneatus
7	Adenanthos	cygnorum
8	Adenanthos	detmoldii
9	Adenanthos	dobagii
10	Adenanthos	dobsonii
11	Adenanthos	drummondii
12	Adenanthos	ellipticus
13	Adenanthos	eyrei
14	Adenanthos	filifolius
15	Adenanthos	flavidiflorus
16	Adenanthos	forrestii
17	Adenanthos	glabrescens
18	Adenanthos	gracilipes
19	Adenanthos	ileticos
20	Adenanthos	labillardierei
21	Adenanthos	linearis
22	Adenanthos	macropodianus
23	Adenanthos	meisneri
24	Adenanthos	obovatus
25	Adenanthos	oreophilus
26	Adenanthos	pungens
27	Adenanthos	sericeus
28	Adenanthos	strictus
29	Adenanthos	terminalis
30	Adenanthos	velutinus
31	Adenanthos	venosus
32	Agastachys	odorata
33	Alloxylon	brachycarpum
34	Alloxylon	flammeum
35	Alloxylon	pinnatum
36	Alloxylon	wickhamii
37	Athertonia	diversifolia
38	Aulax	cancellata
39	Aulax	pallasia
40	Aulax	umbellata
41	Austromuellera	trinervia
42	Austromuellera	valida
43	Banksia	aculeata
44	Banksia	aemula
45	Banksia	aquilonia
46	Banksia	ashbyi
47	Banksia	attenuata
48	Banksia	audax
49	Banksia	baueri
50	Banksia	baxteri
51	Banksia	benthamiana
52	Banksia	blechnifolia
53	Banksia	brownii
54	Banksia	burdettii
55	Banksia	caleyi
56	Banksia	candolleana
57	Banksia	canei
58	Banksia	chamaephyton
59	Banksia	coccinea
60	Banksia	conferta
61	Banksia	croajingolensis
62	Banksia	cuneata
63	Banksia	dentata
64	Banksia	dryandroides
65	Banksia	elderiana
66	Banksia	elegans
67	Banksia	epica
68	Banksia	ericifolia
69	Banksia	ericifolia var. macrantha
70	Banksia	gardneri
71	Banksia	goodii
72	Banksia	grandis
73	Banksia	grossa
74	Banksia	hookeriana
75	Banksia	ilicifolia

	Genus	Species
76	Banksia	incana
77	Banksia	integrifolia
78	Banksia	laevigata
79	Banksia	lanata
80	Banksia	laricina
81	Banksia	leptophylla
82	Banksia	lindleyana
83	Banksia	littoralis
84	Banksia	lullfitzii
85	Banksia	marginata
86	Banksia	media
87	Banksia	meisneri
88	Banksia	menziesii
89	Banksia	micrantha
90	Banksia	nutans
91	Banksia	oblongifolia
92	Banksia	occidentalis
93	Banksia	oligantha
94	Banksia	oreophila
95	Banksia	ornata
96	Banksia	paludosa
97	Banksia	petiolaris
98	Banksia	pilostylis
99	Banksia	plagiocarpa
100	Banksia	praemorsa
101	Banksia	prionotes
102	Banksia	pulchella
103	Banksia	quercifolia
104	Banksia	repens
105	Banksia	robur
106	Banksia	rosserae
107	Banksia	saxicola
108	Banksia	scabrella
109	Banksia	sceptrum
110	Banksia	seminuda
111	Banksia	serrata
112	Banksia	solandri
113	Banksia	speciosa
114	Banksia	sphaerocarpa
115	Banksia	spinulosa
116	Banksia	spinulosa var. cunninghamii
117	Banksia	spinulosa var. collina
118	Banksia	telmatiaea
119	Banksia	tricuspis
120	Banksia	verticillata
121	Banksia	victoriae
122	Banksia	violacea
123	Banksia	acanthopoda
124	Banksia	anatona
125	Banksia	arborea
126	Banksia	arctotidis
127	Banksia	armata
128	Banksia	aurantia
129	Banksia	biterax
130	Banksia	bipinnatifida
131	Banksia	pellaeifolia
132	Banksia	borealis
133	Banksia	brunnea
134	Banksia	calophylla
135	Banksia	carlinoides
136	Banksia	catoglypta
137	Banksia	cirsioides
138	Banksia	columnaris
139	Banksia	comosa
140	Banksia	concinna
141	Banksia	densa
142	Banksia	corvijuga
143	Banksia	obovata
144	Banksia	cynaroides
145	Banksia	cypholoba
146	Banksia	drummondii
147	Banksia	echinata
148	Banksia	epimicta
149	Banksia	erythrocephala
150	Banksia	falcata

	Genus	Species
151	Banksia	fasciculata
152	Banksia	rufa
153	Banksia	fililoba
154	Banksia	foliolata
155	Banksia	foliosissima
156	Banksia	formosa
157	Banksia	fraseri
158	Banksia	fuscobractea
159	Banksia	glaucifolia
160	Banksia	hewardiana
161	Banksia	hirta
162	Banksia	horrida
163	Banksia	idiogenes
164	Banksia	insulanemorecincta
165	Banksia	ionthocarpa
166	Banksia	kippistiana
167	Banksia	lepidorhiza
168	Banksia	dallanneyi
169	Banksia	meganotia
170	Banksia	mimica
171	Banksia	montana
172	Banksia	mucronulata
173	Banksia	nana
174	Banksia	alliacea
175	Banksia	nobilis
176	Banksia	obtusa
177	Banksia	octotriginta
178	Banksia	pallida
179	Banksia	platycarpa
180	Banksia	plumosa
181	Banksia	polycephala
182	Banksia	porrecta
183	Banksia	undata
184	Banksia	acuminata
185	Banksia	prionophylla
186	Banksia	proteoides
187	Banksia	pseudoplumosa
188	Banksia	pteridifolia
189	Banksia	bella
190	Banksia	purdieana
191	Banksia	heliantha
192	Banksia	rufistylis
193	Banksia	sclerophylla
194	Banksia	seneciifolia
195	Banksia	serra
196	Banksia	serratuloides
197	Banksia	sessilis
198	Banksia	shanklandiorum
199	Banksia	shuttleworthiana
200	Banksia	splendida
201	Banksia	squarrosa
202	Banksia	stenoprion
203	Banksia	strictifolia
204	Banksia	stuposa
205	Banksia	subpinnatifida
206	Banksia	subulata
207	Banksia	tenuis
208	Banksia	tortifolia
209	Banksia	tridentata
210	Banksia	trifontinalis
211	Banksia	vestita
212	Banksia	viscida
213	Banksia	wonganensis
214	Banksia	xylothemelia
215	Beauprea	asplenioides
216	Beauprea	balansae
217	Beauprea	comptonii
218	Beauprea	congesta
219	Beauprea	crassifolia
220	Beauprea	filipes
221	Beauprea	gracilis
222	Beauprea	montana
223	Beauprea	montis-fontium
224	Beauprea	neglecta
225	Beauprea	pancheri

	Genus	Species
226	Beauprea	penariensis
227	Beauprea	spathulifolia
228	Beaupreopsis	paniculata
229	Bellendena	montana
230	Bleasdalea	bleasdalei
231	Bleasdalea	papuana
232	Brabejum	stellatifolium
233	Buckinghamia	celsissima
234	Buckinghamia	ferruginiflora
235	Cardwellia	sublimis
236	Carnarvonia	araliifolia
237	Catalepidia	heyana
238	Cenarrhenes	nitida
239	Conospermum	acerosum
240	Conospermum	amoenum
241	Conospermum	boreale
242	Conospermum	brachyphyllum
243	Conospermum	bracteosum
244	Conospermum	brownii
245	Conospermum	burgessiorum
246	Conospermum	caeruleum
247	Conospermum	canaliculatum
248	Conospermum	capitatum
249	Conospermum	cinereum
250	Conospermum	coerulescens
251	Conospermum	crassinervium
252	Conospermum	croniniae
253	Conospermum	densiflorum
254	Conospermum	distichum
255	Conospermum	eatoniae
256	Conospermum	ellipticum
257	Conospermum	ephedroides
258	Conospermum	ericifolium
259	Conospermum	filifolium
260	Conospermum	flexuosum
261	Conospermum	floribundum
262	Conospermum	galeatum
263	Conospermum	glumaceum
264	Conospermum	hookeri
265	Conospermum	huegelii
266	Conospermum	incurvum
267	Conospermum	leianthum
268	Conospermum	longifolium
269	Conospermum	microflorum
270	Conospermum	mitchellii
271	Conospermum	multispicatum
272	Conospermum	nervosum
273	Conospermum	paniculatum
274	Conospermum	patens
275	Conospermum	petiolare
276	Conospermum	polycephalum
277	Conospermum	quadripetalum
278	Conospermum	scaposum
279	Conospermum	sigmoideum
280	Conospermum	spectabile
281	Conospermum	sphacelatum
282	Conospermum	stoechadis
283	Conospermum	taxifolium
284	Conospermum	tenuifolium
285	Conospermum	teretifolium
286	Conospermum	toddii
287	Conospermum	triplinervium
288	Conospermum	undulatum
289	Conospermum	unilaterale
290	Conospermum	wycherleyi
291	Darlingia	darlingiana
292	Darlingia	ferruginea
293	Diastella	buekii
294	Diastella	divaricata
295	Diastella	fraterna
296	Diastella	myrtifolia
297	Diastella	parilis
298	Diastella	proteoides
299	Diastella	thymelaeoides
300	Dilobeia	tenuinervis

	Genus	**Species**
301	Dilobeia	thouarsii
302	Eidothea	hardeniana
303	Eidothea	zoexylocarya
304	Embothrium	coccineum
305	Eucarpha	deplanchei
306	Euplassa	bahiensis
307	Euplassa	cantareirae
308	Euplassa	chimantensis
309	Euplassa	duquei
310	Euplassa	glaziovii
311	Euplassa	hoehnei
312	Euplassa	inaequalis
313	Euplassa	incana
314	Euplassa	isernii
315	Euplassa	itatiaiae
316	Euplassa	legalis
317	Euplassa	madeirae
318	Euplassa	nebularis
319	Euplassa	occidentalis
320	Euplassa	organensis
321	Euplassa	pinnata
322	Euplassa	rufa
323	Euplassa	saxicola
324	Euplassa	semicostata
325	Euplassa	taubertiana
326	Faurea	arborea
327	Faurea	argentea
328	Faurea	coriacea
329	Faurea	delevoyi
330	Faurea	discolor
331	Faurea	forficuliflora
332	Faurea	galpinii
333	Faurea	intermedia
334	Faurea	lucida
335	Faurea	macnaughtonii
336	Faurea	racemosa
337	Faurea	rochetiana
338	Faurea	rubriflora
339	Faurea	saligna
340	Faurea	wentzeliana
341	Finschia	carrii
342	Finschia	chloroxantha
343	Finschia	ferruginiflora
344	Finschia	rufa
345	Floydia	praealta
346	Franklandia	fucifolia
347	Franklandia	triaristata
348	Garnieria	spathulifolia
349	Gevuina	avellana
350	Grevillea	acacioides
351	Grevillea	acanthifolia
352	Grevillea	acerata
353	Grevillea	acrobotrya
354	Grevillea	acropogon
355	Grevillea	acuaria
356	Grevillea	adenotricha
357	Grevillea	agrifolia
358	Grevillea	albiflora
359	Grevillea	alpina
360	Grevillea	alpivaga
361	Grevillea	althoferorum
362	Grevillea	amplexans
363	Grevillea	anethifolia
364	Grevillea	aneura
365	Grevillea	angulata
366	Grevillea	angustiloba
367	Grevillea	annulifera
368	Grevillea	aquifolium
369	Grevillea	arenaria
370	Grevillea	arenaria subsp. canescens
371	Grevillea	argyrophylla
372	Grevillea	armigera
373	Grevillea	asparagoides
374	Grevillea	aspera
375	Grevillea	aspleniifolia

	Genus	Species
376	Grevillea	asteriscosa
377	Grevillea	aurea
378	Grevillea	australis
379	Grevillea	baileyana
380	Grevillea	banksii
381	Grevillea	banyabba
382	Grevillea	barklyana
383	Grevillea	batrachioides
384	Grevillea	baueri
385	Grevillea	baxteri
386	Grevillea	beadleana
387	Grevillea	beardiana
388	Grevillea	bedggoodiana
389	Grevillea	bemboka
390	Grevillea	benthamiana
391	Grevillea	berryana
392	Grevillea	biformis
393	Grevillea	bipinnatifida
394	Grevillea	biternata
395	Grevillea	brachystachya
396	Grevillea	brachystylis
397	Grevillea	bracteosa
398	Grevillea	brevifolia
399	Grevillea	brevis
400	Grevillea	bronweniae
401	Grevillea	buxifolia
402	Grevillea	byrnesii
403	Grevillea	cagiana
404	Grevillea	calcicola
405	Grevillea	caleyi
406	Grevillea	calliantha
407	Grevillea	callichlaena
408	Grevillea	candelabroides
409	Grevillea	candicans
410	Grevillea	candolleana
411	Grevillea	capitellata
412	Grevillea	celata
413	Grevillea	centristigma
414	Grevillea	ceratocarpa
415	Grevillea	cheilocarpa
416	Grevillea	christineae
417	Grevillea	chrysophaea
418	Grevillea	cirsiifolia
419	Grevillea	coccinea
420	Grevillea	commutata
421	Grevillea	concinna
422	Grevillea	confertifolia
423	Grevillea	coriacea
424	Grevillea	corrugata
425	Grevillea	costata
426	Grevillea	crassifolia
427	Grevillea	cravenii
428	Grevillea	crithmifolia
429	Grevillea	crowleyae
430	Grevillea	cunninghamii
431	Grevillea	curviloba
432	Grevillea	cyranostigma
433	Grevillea	decipiens
434	Grevillea	decurrens
435	Grevillea	deflexa
436	Grevillea	delta
437	Grevillea	depauperata
438	Grevillea	didymobotrya
439	Grevillea	dielsiana
440	Grevillea	diffusa
441	Grevillea	dimidiata
442	Grevillea	diminuta
443	Grevillea	dimorpha
444	Grevillea	disjuncta
445	Grevillea	dissecta
446	Grevillea	divaricata
447	Grevillea	diversifolia
448	Grevillea	dolichopoda
449	Grevillea	donaldiana
450	Grevillea	drummondii

	Genus	Species
451	Grevillea	dryandri
452	Grevillea	dryandroides
453	Grevillea	dryophylla
454	Grevillea	dunlopii
455	Grevillea	elbertii
456	Grevillea	elongata
457	Grevillea	endlicheriana
458	Grevillea	epicroca
459	Grevillea	erectiloba
460	Grevillea	eremophila
461	Grevillea	erinacea
462	Grevillea	eriobotrya
463	Grevillea	eriostachya
464	Grevillea	eryngioides
465	Grevillea	erythroclada
466	Grevillea	evanescens
467	Grevillea	evansiana
468	Grevillea	excelsior
469	Grevillea	exposita
470	Grevillea	extorris
471	Grevillea	exul
472	Grevillea	fasciculata
473	Grevillea	fastigiata
474	Grevillea	fililoba
475	Grevillea	fistulosa
476	Grevillea	flexuosa
477	Grevillea	floribunda
478	Grevillea	florida
479	Grevillea	floripendula
480	Grevillea	formosa
481	Grevillea	fulgens
482	Grevillea	fuscolutea
483	Grevillea	gariwerdensis
484	Grevillea	georgeana
485	Grevillea	gillivrayi
486	Grevillea	glabrescens
487	Grevillea	glauca
488	Grevillea	globosa
489	Grevillea	glossadenia
490	Grevillea	goodii
491	Grevillea	gordoniana
492	Grevillea	granulifera
493	Grevillea	granulosa
494	Grevillea	guthrieana
495	Grevillea	hakeoides
496	Grevillea	halmaturina
497	Grevillea	haplantha
498	Grevillea	heliosperma
499	Grevillea	helmsiae
500	Grevillea	hilliana
501	Grevillea	hirtella
502	Grevillea	hislopii
503	Grevillea	hockingsii
504	Grevillea	hodgei
505	Grevillea	hookeriana
506	Grevillea	huegelii
507	Grevillea	humifusa
508	Grevillea	humilis
509	Grevillea	iaspicula
510	Grevillea	ilicifolia
511	Grevillea	imberbis
512	Grevillea	inconspicua
513	Grevillea	incrassata
514	Grevillea	incurva
515	Grevillea	infecunda
516	Grevillea	infundibularis
517	Grevillea	insignis
518	Grevillea	integrifolia
519	Grevillea	intricata
520	Grevillea	involucrata
521	Grevillea	irrasa
522	Grevillea	jephcottii
523	Grevillea	johnsonii
524	Grevillea	juncifolia
525	Grevillea	juniperina

	Genus	Species
526	Grevillea	juniperina subsp. amphitricha
527	Grevillea	juniperina subsp. sulphurea
528	Grevillea	kedumbensis
529	Grevillea	kenneallyi
530	Grevillea	kennedyana
531	Grevillea	kirkalocka
532	Grevillea	lanigera
533	Grevillea	latifolia
534	Grevillea	laurifolia
535	Grevillea	lavandulacea
536	Grevillea	leiophylla
537	Grevillea	leptobotrys
538	Grevillea	leptopoda
539	Grevillea	leucoclada
540	Grevillea	leucopteris
541	Grevillea	levis
542	Grevillea	linearifolia
543	Grevillea	linsmithii
544	Grevillea	lissopleura
545	Grevillea	longicuspis
546	Grevillea	longifolia
547	Grevillea	longistyla
548	Grevillea	lullfitzii
549	Grevillea	maccutcheonii
550	Grevillea	macleayana
551	Grevillea	maherae
552	Grevillea	makinsonii
553	Grevillea	manglesii
554	Grevillea	manglesii subsp. ornithopoda
555	Grevillea	manglesioides
556	Grevillea	marriottii
557	Grevillea	masonii
558	Grevillea	maxwellii
559	Grevillea	meisneri
560	Grevillea	metamorpha
561	Grevillea	micrantha
562	Grevillea	microstegia
563	Grevillea	microstyla
564	Grevillea	mimosoides
565	Grevillea	miniata
566	Grevillea	minutiflora
567	Grevillea	miqueliana
568	Grevillea	mollis
569	Grevillea	molyneuxii
570	Grevillea	monslacana
571	Grevillea	montana
572	Grevillea	monticola
573	Grevillea	montis-cole
574	Grevillea	mucronulata
575	Grevillea	muelleri
576	Grevillea	murex
577	Grevillea	muricata
578	Grevillea	myosodes
579	Grevillea	nana
580	Grevillea	nematophylla
581	Grevillea	neurophylla
582	Grevillea	newbeyi
583	Grevillea	nudiflora
584	Grevillea	obliquistigma
585	Grevillea	obtecta
586	Grevillea	obtusiflora
587	Grevillea	obtusifolia
588	Grevillea	occidentalis
589	Grevillea	oldei
590	Grevillea	oleoides
591	Grevillea	oligantha
592	Grevillea	oligomera
593	Grevillea	olivacea
594	Grevillea	oncogyne
595	Grevillea	oxyantha
596	Grevillea	pachylostyla
597	Grevillea	paniculata
598	Grevillea	papillosa
599	Grevillea	papuana
600	Grevillea	paradoxa

	Genus	Species
601	Grevillea	parallela
602	Grevillea	parallelinervis
603	Grevillea	parviflora
604	Grevillea	parvula
605	Grevillea	patentiloba
606	Grevillea	patulifolia
607	Grevillea	pauciflora
608	Grevillea	pectinata
609	Grevillea	petrophiloides
610	Grevillea	phanerophlebia
611	Grevillea	phillipsiana
612	Grevillea	pilosa
613	Grevillea	pilulifera
614	Grevillea	pimeleoides
615	Grevillea	pinaster
616	Grevillea	pinifolia
617	Grevillea	pityophylla
618	Grevillea	pluricaulis
619	Grevillea	plurijuga
620	Grevillea	polyacida
621	Grevillea	polybotrya
622	Grevillea	polybractea
623	Grevillea	prasina
624	Grevillea	preissii
625	Grevillea	prominens
626	Grevillea	prostrata
627	Grevillea	psilantha
628	Grevillea	pteridifolia
629	Grevillea	pterosperma
630	Grevillea	pulchella
631	Grevillea	punctata
632	Grevillea	pungens
633	Grevillea	pyramidalis
634	Grevillea	pythara
635	Grevillea	quadricauda
636	Grevillea	quercifolia
637	Grevillea	quinquenervis
638	Grevillea	ramosissima
639	Grevillea	rara
640	Grevillea	raybrownii
641	Grevillea	refracta
642	Grevillea	renwickiana
643	Grevillea	repens
644	Grevillea	reptans
645	Grevillea	rhizomatosa
646	Grevillea	rhyolitica
647	Grevillea	rigida
648	Grevillea	ripicola
649	Grevillea	rivularis
650	Grevillea	robusta
651	Grevillea	rogersoniana
652	Grevillea	rosieri
653	Grevillea	rosmarinifolia
654	Grevillea	rosmarinifolia subsp. glabella
655	Grevillea	roycei
656	Grevillea	rubicunda
657	Grevillea	rudis
658	Grevillea	saccata
659	Grevillea	sarissa
660	Grevillea	scabra
661	Grevillea	scabrida
662	Grevillea	scapigera
663	Grevillea	scortechinii
664	Grevillea	secunda
665	Grevillea	sericea
666	Grevillea	sessilis
667	Grevillea	shiressii
668	Grevillea	shuttleworthiana
669	Grevillea	singuliflora
670	Grevillea	sparsiflora
671	Grevillea	speciosa
672	Grevillea	sphacelata
673	Grevillea	spinosa
674	Grevillea	spinosissima
675	Grevillea	squiresiae

	Genus	Species
676	Grevillea	steiglitziana
677	Grevillea	stenobotrya
678	Grevillea	stenogyne
679	Grevillea	stenomera
680	Grevillea	stenostachya
681	Grevillea	striata
682	Grevillea	subterlineata
683	Grevillea	subtiliflora
684	Grevillea	sulcata
685	Grevillea	synapheae
686	Grevillea	tenuiflora
687	Grevillea	tenuiloba
688	Grevillea	teretifolia
689	Grevillea	tetragonoloba
690	Grevillea	tetrapleura
691	Grevillea	thelemanniana
692	Grevillea	thyrsoides
693	Grevillea	trachytheca
694	Grevillea	tridentifera
695	Grevillea	treueriana
696	Grevillea	trifida
697	Grevillea	triloba
698	Grevillea	tripartita
699	Grevillea	triternata
700	Grevillea	umbellulata
701	Grevillea	uncinulata
702	Grevillea	uniformis
703	Grevillea	variifolia
704	Grevillea	velutinella
705	Grevillea	venusta
706	Grevillea	versicolor
707	Grevillea	vestita
708	Grevillea	victoriae
709	Grevillea	virgata
710	Grevillea	viridiflava
711	Grevillea	whiteana
712	Grevillea	wickhamii
713	Grevillea	wilkinsonii
714	Grevillea	willisii
715	Grevillea	wilsonii
716	Grevillea	wiradjuri
717	Grevillea	wittweri
718	Grevillea	xiphoidea
719	Grevillea	yorkrakinensis
720	Grevillea	zygoloba
721	Hakea	actites
722	Hakea	aculeata
723	Hakea	acuminata
724	Hakea	adnata
725	Hakea	aenigma
726	Hakea	ambigua
727	Hakea	amplexicaulis
728	Hakea	anadenia
729	Hakea	arborescens
730	Hakea	archaeoides
731	Hakea	asperma
732	Hakea	auriculata
733	Hakea	bakeriana
734	Hakea	baxteri
735	Hakea	bicornata
736	Hakea	brachyptera
737	Hakea	brownii
738	Hakea	bucculenta
739	Hakea	candolleana
740	Hakea	carinata
741	Hakea	ceratophylla
742	Hakea	chordophylla
743	Hakea	chromatropa
744	Hakea	cinerea
745	Hakea	circumalata
746	Hakea	clavata
747	Hakea	collina
748	Hakea	commutata
749	Hakea	conchifolia
750	Hakea	constablei

	Genus	Species
751	Hakea	corymbosa
752	Hakea	costata
753	Hakea	cristata
754	Hakea	cucullata
755	Hakea	cyclocarpa
756	Hakea	cycloptera
757	Hakea	cygna
758	Hakea	dactyloides
759	Hakea	denticulata
760	Hakea	decurrens
761	Hakea	divaricata
762	Hakea	dohertyi
763	Hakea	drupacea
764	Hakea	elliptica
765	Hakea	ednieana
766	Hakea	eneabba
767	Hakea	epiglottis
768	Hakea	erecta
769	Hakea	eriantha
770	Hakea	erinacea
771	Hakea	eyreana
772	Hakea	falcata
773	Hakea	ferruginea
774	Hakea	flabellifolia
775	Hakea	florida
776	Hakea	florulenta
777	Hakea	francisiana
778	Hakea	fraseri
779	Hakea	gibbosa
780	Hakea	gilbertii
781	Hakea	grammatophylla
782	Hakea	hastata
783	Hakea	hookeriana
784	Hakea	horrida
785	Hakea	ilicifolia
786	Hakea	incrassata
787	Hakea	invaginata
788	Hakea	ivoryi
789	Hakea	kippistiana
790	Hakea	laevipes
791	Hakea	lasiantha
792	Hakea	lasianthoides
793	Hakea	lasiocarpha
794	Hakea	laurina
795	Hakea	lehmanniana
796	Hakea	leucoptera
797	Hakea	linearis
798	Hakea	lissocarpha
799	Hakea	lissosperma
800	Hakea	longiflora
801	Hakea	loranthifolia
802	Hakea	lorea
803	Hakea	maconochieana
804	Hakea	macraeana
805	Hakea	macrocarpa
806	Hakea	macrorhyncha
807	Hakea	marginata
808	Hakea	megadenia
809	Hakea	megalosperma
810	Hakea	meisneriana
811	Hakea	microcarpa
812	Hakea	minyma
813	Hakea	mitchellii
814	Hakea	multilineata
815	Hakea	myrtoides
816	Hakea	neurophylla
817	Hakea	newbeyana
818	Hakea	nitida
819	Hakea	nodosa
820	Hakea	obliqua
821	Hakea	obtusa
822	Hakea	ochroptera
823	Hakea	oleifolia
824	Hakea	orthorrhyncha
825	Hakea	pachyphylla

	Genus	Species
826	Hakea	pandanicarpa
827	Hakea	pandanicarpa subsp. crassifolia
828	Hakea	pedunculata
829	Hakea	pendens
830	Hakea	persiehana
831	Hakea	petiolaris
832	Hakea	platysperma
833	Hakea	plurinervia
834	Hakea	polyanthema
835	Hakea	preissii
836	Hakea	pritzelii
837	Hakea	propinqua
838	Hakea	prostrata
839	Hakea	psilorrhyncha
840	Hakea	pulvinifera
841	Hakea	purpurea
842	Hakea	pycnoneura
843	Hakea	recurva
844	Hakea	repullulans
845	Hakea	rhombales
846	Hakea	rigida
847	Hakea	rostrata
848	Hakea	rugosa
849	Hakea	ruscifolia
850	Hakea	salicifolia
851	Hakea	scoparia
852	Hakea	sericea
853	Hakea	smilacifolia
854	Hakea	spathulata
855	Hakea	standleyensis
856	Hakea	stenocarpa
857	Hakea	stenophylla
858	Hakea	strumosa
859	Hakea	subsulcata
860	Hakea	sulcata
861	Hakea	teretifolia
862	Hakea	tephrosperma
863	Hakea	trifurcata
864	Hakea	trineura
865	Hakea	tuberculata
866	Hakea	undulata
867	Hakea	ulicina
868	Hakea	varia
869	Hakea	verrucosa
870	Hakea	victoriae
871	Hakea	vittata
872	Helicia	acutifolia
873	Helicia	albiflora
874	Helicia	amplifolia
875	Helicia	attenuata
876	Helicia	australasica
877	Helicia	calocoma
878	Helicia	cauliflora
879	Helicia	clivicola
880	Helicia	cochinchinensis
881	Helicia	dongxingensis
882	Helicia	excelsa
883	Helicia	formosana
884	Helicia	fuscotomentosa
885	Helicia	glabriflora
886	Helicia	grandis
887	Helicia	grandifolia
888	Helicia	hainanensis
889	Helicia	insularis
890	Helicia	kwangtungensis
891	Helicia	latifolia
892	Helicia	longipetiolata
893	Helicia	maxwelliana
894	Helicia	moluccana
895	Helicia	neglecta
896	Helicia	nilagirica
897	Helicia	obovatifolia
898	Helicia	peekelii
899	Helicia	peltata
900	Helicia	petiolaris

	Genus	Species
901	Helicia	polyosmoides
902	Helicia	pterygota
903	Helicia	pyrrhobotrya
904	Helicia	rengetiensis
905	Helicia	reticulata
906	Helicia	retusa
907	Helicia	robusta
908	Helicia	rostrata
909	Helicia	shweliensis
910	Helicia	silvicola
911	Helicia	tibetensis
912	Helicia	tsaii
913	Helicia	vestita
914	Heliciopsis	artocarpoides
915	Heliciopsis	cockburnii
916	Heliciopsis	henryi
917	Heliciopsis	incisa
918	Heliciopsis	lanceolata
919	Heliciopsis	litseifolia
920	Heliciopsis	lobata
921	Heliciopsis	mahmudii
922	Heliciopsis	montana
923	Heliciopsis	percoriacea
924	Heliciopsis	rufidula
925	Heliciopsis	terminalis
926	Heliciopsis	velutina
927	Heliciopsis	whitmorei
928	Hicksbeachia	pilosa
929	Hicksbeachia	pinnatifolia
930	Hollandaea	sayeriana
931	Hollandaea	riparia
932	Isopogon	adenanthoides
933	Isopogon	alcicornis
934	Isopogon	anethifolius
935	Isopogon	anemonifolius
936	Isopogon	asper
937	Isopogon	attenuatus
938	Isopogon	axillaris
939	Isopogon	baxteri
940	Isopogon	buxifolius
941	Isopogon	ceratophyllus
942	Isopogon	cuneatus
943	Isopogon	dawsonii
944	Isopogon	divergens
945	Isopogon	drummondii
946	Isopogon	dubius
947	Isopogon	fletcheri
948	Isopogon	formosus
949	Isopogon	inconspicuus
950	Isopogon	latifolius
951	Isopogon	linearis
952	Isopogon	longifolius
953	Isopogon	petiolaris
954	Isopogon	polycephalus
955	Isopogon	prostratus
956	Isopogon	scabriusculus
957	Isopogon	sphaerocephalus
958	Isopogon	teretifolius
959	Isopogon	tridens
960	Isopogon	trilobus
961	Isopogon	uncinatus
962	Isopogon	villosus
963	Kermadecia	elliptica
964	Kermadecia	pronyensis
965	Kermadecia	rotundifolia
966	Kermadecia	sinuata
967	Knightia	excelsa
968	Lambertia	echinata
969	Lambertia	ericifolia
970	Lambertia	fairallii
971	Lambertia	formosa
972	Lambertia	ilicifolia
973	Lambertia	inermis
974	Lambertia	multiflora
975	Lambertia	orbifolia

	Genus	**Species**
976	Lambertia	rariflora
977	Lambertia	uniflora
978	Leucadendron	album
979	Leucadendron	arcuatum
980	Leucadendron	argenteum
981	Leucadendron	barkerae
982	Leucadendron	bonum
983	Leucadendron	brunioides
984	Leucadendron	burchellii
985	Leucadendron	cadens
986	Leucadendron	chamelaea
987	Leucadendron	cinereum
988	Leucadendron	comosum
989	Leucadendron	concavum
990	Leucadendron	conicum
991	Leucadendron	coniferum
992	Leucadendron	cordatum
993	Leucadendron	coriaceum
994	Leucadendron	corymbosum
995	Leucadendron	cryptocephalum
996	Leucadendron	daphnoides
997	Leucadendron	diemontianum
998	Leucadendron	discolor
999	Leucadendron	dregei
1000	Leucadendron	dubium
1001	Leucadendron	elimense
1002	Leucadendron	ericifolium
1003	Leucadendron	eucalyptifolium
1004	Leucadendron	flexuosum
1005	Leucadendron	floridum
1006	Leucadendron	foedum
1007	Leucadendron	galpinii
1008	Leucadendron	gandogeri
1009	Leucadendron	glaberrimum
1010	Leucadendron	globosum
1011	Leucadendron	grandiflorum
1012	Leucadendron	gydoense
1013	Leucadendron	immoderatum
1014	Leucadendron	lanigerum
1015	Leucadendron	laureolum
1016	Leucadendron	laxum
1017	Leucadendron	levisanus
1018	Leucadendron	linifolium
1019	Leucadendron	loeriense
1020	Leucadendron	loranthifolium
1021	Leucadendron	macowanii
1022	Leucadendron	meridianum
1023	Leucadendron	meyerianum
1024	Leucadendron	microcephalum
1025	Leucadendron	modestum
1026	Leucadendron	muirii
1027	Leucadendron	nervosum
1028	Leucadendron	nitidum
1029	Leucadendron	nobile
1030	Leucadendron	olens
1031	Leucadendron	orientale
1032	Leucadendron	osbornei
1033	Leucadendron	platyspermum
1034	Leucadendron	pondoense
1035	Leucadendron	procerum
1036	Leucadendron	pubescens
1037	Leucadendron	pubibracteolatum
1038	Leucadendron	radiatum
1039	Leucadendron	remotum
1040	Leucadendron	roodii
1041	Leucadendron	rourkei
1042	Leucadendron	rubrum
1043	Leucadendron	salicifolium
1044	Leucadendron	salignum
1045	Leucadendron	sericeum
1046	Leucadendron	sessile
1047	Leucadendron	sheilae
1048	Leucadendron	singulare
1049	Leucadendron	sorocephalodes
1050	Leucadendron	spirale

	Genus	Species
1051	Leucadendron	spissifolium
1052	Leucadendron	stellare
1053	Leucadendron	stelligerum
1054	Leucadendron	strobilinum
1055	Leucadendron	teretifolium
1056	Leucadendron	thymifolium
1057	Leucadendron	tinctum
1058	Leucadendron	tradouwense
1059	Leucadendron	uliginosum
1060	Leucadendron	verticillatum
1061	Leucadendron	xanthoconus
1062	Leucospermum	arenarium
1063	Leucospermum	bolusii
1064	Leucospermum	calligerum
1065	Leucospermum	catherinae
1066	Leucospermum	conocarpodendron
1067	Leucospermum	cordatum
1068	Leucospermum	cordifolium
1069	Leucospermum	cuneiforme
1070	Leucospermum	erubescens
1071	Leucospermum	formosum
1072	Leucospermum	fulgens
1073	Leucospermum	gerrardii
1074	Leucospermum	glabrum
1075	Leucospermum	gracile
1076	Leucospermum	grandiflorum
1077	Leucospermum	gueinzii
1078	Leucospermum	hamatum
1079	Leucospermum	harpagonatum
1080	Leucospermum	heterophyllum
1081	Leucospermum	hypophyllocarpodendron
1082	Leucospermum	innovans
1083	Leucospermum	lineare
1084	Leucospermum	muirii
1085	Leucospermum	mundii
1086	Leucospermum	oleifolium
1087	Leucospermum	parile
1088	Leucospermum	patersonii
1089	Leucospermum	pedunculatum
1090	Leucospermum	pluridens
1091	Leucospermum	praecox
1092	Leucospermum	praemorsum
1093	Leucospermum	profugum
1094	Leucospermum	prostratum
1095	Leucospermum	reflexum
1096	Leucospermum	rodolentum
1097	Leucospermum	royenifolium
1098	Leucospermum	saxatile
1099	Leucospermum	saxosum
1100	Leucospermum	secundifolium
1101	Leucospermum	spathulatum
1102	Leucospermum	tomentosum
1103	Leucospermum	tottum
1104	Leucospermum	truncatulum
1105	Leucospermum	truncatum
1106	Leucospermum	utriculosum
1107	Leucospermum	vestitum
1108	Leucospermum	winteri
1109	Leucospermum	wittebergensis
1110	Lomatia	arborescens
1111	Lomatia	dentata
1112	Lomatia	ferruginea
1113	Lomatia	fraseri
1114	Lomatia	fraxinifolia
1115	Lomatia	hirsuta
1116	Lomatia	ilicifolia
1117	Lomatia	myricoides
1118	Lomatia	polymorpha
1119	Lomatia	silaifolia
1120	Lomatia	tasmanica
1121	Lomatia	tinctoria
1122	Macadamia	claudiensis
1123	Macadamia	grandis
1124	Macadamia	hildebrandii
1125	Macadamia	integrifolia

	Genus	Species
1126	Macadamia	jansenii
1127	Macadamia	ternifolia
1128	Macadamia	tetraphylla
1129	Macadamia	whelanii
1130	Macadamia	neurophylla
1131	Malagasia	alticola
1132	Megahertzia	amplexicaulis
1133	Mimetes	arboreus
1134	Mimetes	argenteus
1135	Mimetes	capitulatus
1136	Mimetes	chrysanthus
1137	Mimetes	cucullatus
1138	Mimetes	fimbrifolius
1139	Mimetes	hirtus
1140	Mimetes	hottentoticus
1141	Mimetes	palustris
1142	Mimetes	pauciflorus
1143	Mimetes	saxatilis
1144	Mimetes	splendidus
1145	Mimetes	stokoei
1146	Musgravea	stenostachya
1147	Musgravea	heterophylla
1148	Neorites	kevediana
1149	Opisthiolepis	heterophylla
1150	Oreocallis	grandiflora

	Genus	Species
1151	Orites	acicularis
1152	Orites	diversifolius
1153	Orites	excelsus
1154	Orites	fiebrigii
1155	Orites	lancifolius
1156	Orites	milliganii
1157	Orites	myrtoidea
1158	Orites	revolutus
1159	Orothamnus	zeyheri
1160	Panopsis	cinnamomea
1161	Panopsis	mucronata
1162	Panopsis	multiflora
1163	Panopsis	parimensis
1164	Panopsis	pearcei
1165	Panopsis	polystachya
1166	Panopsis	ptariana
1167	Panopsis	rubescens
1168	Panopsis	sessilifolia
1169	Panopsis	suaveolens
1170	Panopsis	tepuiana
1171	Panopsis	yolombo
1172	Paranomus	abrotanifolius
1173	Paranomus	adiantifolius
1174	Paranomus	bolusii
1175	Paranomus	bracteolaris

	Genus	Species
1176	Paranomus	candicans
1177	Paranomus	capitatus
1178	Paranomus	centaureoides
1179	Paranomus	dispersus
1180	Paranomus	dregei
1181	Paranomus	esterhuyseniae
1182	Paranomus	lagopus
1183	Paranomus	longicaulis
1184	Paranomus	reflexus
1185	Paranomus	roodebergensis
1186	Paranomus	sceptrum-gustavianus
1187	Paranomus	spathulatus
1188	Paranomus	spicatus
1189	Paranomus	tomentosus
1190	Persoonia	inconspicua
1191	Persoonia	brevirhachis
1192	Persoonia	rufiflora
1193	Persoonia	laurina
1194	Persoonia	confertiflora
1195	Persoonia	silvatica
1196	Persoonia	longifolia
1197	Persoonia	elliptica
1198	Persoonia	arborea
1199	Persoonia	subvelutina
1200	Persoonia	gunnii

	Genus	Species		Genus	Species		Genus	Species
1201	Persoonia	muelleri	1226	Persoonia	katerae	1251	Persoonia	coriacea
1202	Persoonia	moscalii	1227	Persoonia	adenantha	1252	Persoonia	helix
1203	Persoonia	juniperina	1228	Persoonia	stradbrokensis	1253	Persoonia	pertinax
1204	Persoonia	chamaepeuce	1229	Persoonia	prostrata	1254	Persoonia	cymbifolia
1205	Persoonia	virgata	1230	Persoonia	conjuncta	1255	Persoonia	leucopogon
1206	Persoonia	tenuifolia	1231	Persoonia	media	1256	Persoonia	pungens
1207	Persoonia	acerosa	1232	Persoonia	iogyna	1257	Persoonia	baeckeoides
1208	Persoonia	myrtilloides	1233	Persoonia	tropica	1258	Persoonia	cordifolia
1209	Persoonia	brevifolia	1234	Persoonia	amaliae	1259	Persoonia	dillwynioides
1210	Persoonia	acuminata	1235	Persoonia	volcanica	1260	Persoonia	flexifolia
1211	Persoonia	recedens	1236	Persoonia	hirsuta	1261	Persoonia	graminea
1212	Persoonia	oxycoccoides	1237	Persoonia	chamaepitys	1262	Persoonia	micranthera
1213	Persoonia	asperula	1238	Persoonia	sericea	1263	Persoonia	chapmaniana
1214	Persoonia	microphylla	1239	Persoonia	fastigiata	1264	Persoonia	pentasticha
1215	Persoonia	terminalis	1240	Persoonia	subtilis	1265	Persoonia	trinervis
1216	Persoonia	bargoensis	1241	Persoonia	curvifolia	1266	Persoonia	angustiflora
1217	Persoonia	nutans	1242	Persoonia	cuspidifera	1267	Persoonia	papillosa
1218	Persoonia	laxa	1243	Persoonia	rigida	1268	Persoonia	bowgada
1219	Persoonia	oblongata	1244	Persoonia	mollis	1269	Persoonia	hexagona
1220	Persoonia	marginata	1245	Persoonia	lanceolata	1270	Persoonia	spathulata
1221	Persoonia	daphnoides	1246	Persoonia	glaucescens	1271	Persoonia	scabra
1222	Persoonia	procumbens	1247	Persoonia	levis	1272	Persoonia	quinquenervis
1223	Persoonia	oleoides	1248	Persoonia	linearis	1273	Persoonia	striata
1224	Persoonia	rufa	1249	Persoonia	pinifolia	1274	Persoonia	sulcata
1225	Persoonia	cornifolia	1250	Persoonia	isophylla	1275	Persoonia	acicularis

	Genus	Species
1276	Persoonia	rudis
1277	Persoonia	filiformis
1278	Persoonia	falcata
1279	Persoonia	biglandulosa
1280	Persoonia	brachystylis
1281	Persoonia	kararae
1282	Persoonia	stricta
1283	Persoonia	saundersiana
1284	Persoonia	teretifolia
1285	Persoonia	comata
1286	Persoonia	saccata
1287	Persoonia	hakeiformis
1288	Petrophile	acicularis
1289	Petrophile	aculeata
1290	Petrophile	anceps
1291	Petrophile	antecedens
1292	Petrophile	arcuata
1293	Petrophile	aspera
1294	Petrophile	axillaris
1295	Petrophile	biloba
1296	Petrophile	biternata
1297	Petrophile	brevifolia
1298	Petrophile	canescens
1299	Petrophile	carduacea
1300	Petrophile	chrysantha
1301	Petrophile	circinata
1302	Petrophile	clavata
1303	Petrophile	conifera
1304	Petrophile	crispata
1305	Petrophile	cyathiforma
1306	Petrophile	divaricata
1307	Petrophile	diversifolia
1308	Petrophile	drummondii
1309	Petrophile	ericifolia
1310	Petrophile	fastigiata
1311	Petrophile	filifolia
1312	Petrophile	glauca
1313	Petrophile	helicophylla
1314	Petrophile	heterophylla
1315	Petrophile	imbricata
1316	Petrophile	incurvata
1317	Petrophile	juncifolia
1318	Petrophile	latericola
1319	Petrophile	linearis
1320	Petrophile	longifolia
1321	Petrophile	macrostachya
1322	Petrophile	media
1323	Petrophile	megalostegia
1324	Petrophile	merrallii
1325	Petrophile	misturata
1326	Petrophile	multisecta
1327	Petrophile	nivea
1328	Petrophile	pauciflora
1329	Petrophile	pedunculata
1330	Petrophile	phylicoides
1331	Petrophile	pilostyla
1332	Petrophile	plumosa
1333	Petrophile	prostrata
1334	Petrophile	pulchella
1335	Petrophile	recurva
1336	Petrophile	rigida
1337	Petrophile	scabriuscula
1338	Petrophile	semifurcata
1339	Petrophile	seminuda
1340	Petrophile	serruriae
1341	Petrophile	sessilis
1342	Petrophile	shirleyae
1343	Petrophile	shuttleworthiana
1344	Petrophile	squamata
1345	Petrophile	striata
1346	Petrophile	stricta
1347	Petrophile	teretifolia
1348	Petrophile	trifurcata
1349	Petrophile	wonganensis
1350	Placospermum	coriaceum

	Genus	**Species**
1351	Protea	caffra
1352	Protea	dracomontana
1353	Protea	glabra
1354	Protea	inopina
1355	Protea	nitida
1356	Protea	nubigena
1357	Protea	parvula
1358	Protea	petiolaris
1359	Protea	rupicola
1360	Protea	simplex
1361	Protea	decurrens
1362	Protea	enervis
1363	Protea	angolensis
1364	Protea	comptonii
1365	Protea	curvata
1366	Protea	laetans
1367	Protea	madiensis
1368	Protea	rubropilosa
1369	Protea	rupestris
1370	Protea	welwitschii
1371	Protea	asymmetrica
1372	Protea	wentzeliana
1373	Protea	cynaroides
1374	Protea	cryophila
1375	Protea	pruinosa
1376	Protea	scabriuscula
1377	Protea	scolopendriifolia
1378	Protea	burchellii
1379	Protea	compacta
1380	Protea	cordata
1381	Protea	eximia
1382	Protea	longifolia
1383	Protea	obtusifolia
1384	Protea	pudens
1385	Protea	roupelliae
1386	Protea	susannae
1387	Protea	aristata
1388	Protea	lanceolata
1389	Protea	repens
1390	Protea	coronata
1391	Protea	grandiceps
1392	Protea	holosericea
1393	Protea	laurifolia
1394	Protea	denticulata
1395	Protea	lorifolia
1396	Protea	magnifica
1397	Protea	neriifolia
1398	Protea	speciosa
1399	Protea	stokoei
1400	Protea	aurea
1401	Protea	aurea subsp. potbergensis
1402	Protea	lacticolor
1403	Protea	mundii
1404	Protea	punctata
1405	Protea	subvestita
1406	Protea	aristata
1407	Protea	venusta
1408	Protea	acaulos
1409	Protea	convexa
1410	Protea	laevis
1411	Protea	revoluta
1412	Protea	ungustata
1413	Protea	foliosa
1414	Protea	intonsa
1415	Protea	montana
1416	Protea	tenax
1417	Protea	vogtsiae
1418	Protea	acuminata
1419	Protea	canaliculata
1420	Protea	nana
1421	Protea	pityphylla
1422	Protea	scolymocephala
1423	Protea	witzenbergiana
1424	Protea	amplexicaulis
1425	Protea	namaquana

	Genus	Species		Genus	Species		Genus	Species
1426	Protea	pendula	1451	Roupala	longepetiolata	1476	Serruria	brownii
1427	Protea	recondita	1452	Roupala	macrophylla	1477	Serruria	candicans
1428	Protea	sulphurea	1453	Roupala	meisneri	1478	Serruria	collina
1429	Protea	caespitosa	1454	Roupala	minima	1479	Serruria	confragosa
1430	Protea	aspera	1455	Roupala	monosperma	1480	Serruria	cyanoides
1431	Protea	lepidocarpodendron	1456	Roupala	montana	1481	Serruria	cygnea
1432	Protea	effusa	1457	Roupala	montana var. paraensis	1482	Serruria	decipiens
1433	Protea	eximia	1458	Roupala	nitida	1483	Serruria	decumbens
1434	Protea	gaguedi	1459	Roupala	obtusata	1484	Serruria	deluvialis
1435	Protea	lorea	1460	Roupala	pachypoda	1485	Serruria	dodii
1436	Protea	piscina	1461	Roupala	pallida	1486	Serruria	effusa
1437	Protea	restionifolia	1462	Roupala	percoriacea	1487	Serruria	elongata
1438	Protea	scabra	1463	Roupala	pseudocordata	1488	Serruria	fasciflora
1439	Protea	scorzonerifolia	1464	Roupala	sculpta	1489	Serruria	flagellifolia
1440	Roupala	asplenioides	1465	Roupala	sororopana	1490	Serruria	flava
1441	Roupala	barnettiae	1466	Roupala	sphenophyllum	1491	Serruria	florida
1442	Roupala	brachybotrys	1467	Roupala	spicata	1492	Serruria	fucifolia
1443	Roupala	brachybotrys subsp. grossidentata	1468	Roupala	suaveolens	1493	Serruria	furcellata
1444	Roupala	consimilis	1469	Serruria	acrocarpa	1494	Serruria	glomerata
1445	Roupala	cordifolia	1470	Serruria	adscendens	1495	Serruria	gremialis
1446	Roupala	dielsii	1471	Serruria	aemula	1496	Serruria	heterophylla
1447	Roupala	ferruginea	1472	Serruria	aitonii	1497	Serruria	hirsuta
1448	Roupala	glaberrima	1473	Serruria	altiscapa	1498	Serruria	inconspicua
1449	Roupala	jelskii	1474	Serruria	balanocephala	1499	Serruria	incrassata
1450	Roupala	lucens	1475	Serruria	bolusii	1500	Serruria	kraussii

	Genus	Species
1501	Serruria	lacunosa
1502	Serruria	leipoldtii
1503	Serruria	linearis
1504	Serruria	meisneriana
1505	Serruria	millefolia
1506	Serruria	nervosa
1507	Serruria	nivenii
1508	Serruria	pedunculata
1509	Serruria	phylicoides
1510	Serruria	pinnata
1511	Serruria	rebeloi
1512	Serruria	reflexa
1513	Serruria	rosea
1514	Serruria	roxburghii
1515	Serruria	rubricaulis
1516	Serruria	scoparia
1517	Serruria	stellata
1518	Serruria	trilopha
1519	Serruria	triternata
1520	Serruria	villosa
1521	Serruria	viridifolia
1522	Serruria	williamsii
1523	Serruria	zeyheri
1524	Sleumerodendron	austrocaledonicum
1525	Sorocephalus	alopecurus
1526	Sorocephalus	capitatus
1527	Sorocephalus	clavigerus
1528	Sorocephalus	crassifolius
1529	Sorocephalus	imbricatus
1530	Sorocephalus	lanatus
1531	Sorocephalus	palustris
1532	Sorocephalus	pinifolius
1533	Sorocephalus	scabridus
1534	Sorocephalus	tenuifolius
1535	Sorocephalus	teretifolius
1536	Spatalla	argentea
1537	Spatalla	barbigera
1538	Spatalla	caudata
1539	Spatalla	colorata
1540	Spatalla	confusa
1541	Spatalla	curvifolia
1542	Spatalla	ericoides
1543	Spatalla	incurva
1544	Spatalla	longifolia
1545	Spatalla	mollis
1546	Spatalla	nubicola
1547	Spatalla	parilis
1548	Spatalla	prolifera
1549	Spatalla	propinqua
1550	Spatalla	racemosa
1551	Spatalla	salsoloides
1552	Spatalla	setacea
1553	Spatalla	squamata
1554	Spatalla	thyrsiflora
1555	Spatalla	tulbaghensis
1556	Sphalmium	racemosum
1557	Stenocarpus	acacioides
1558	Stenocarpus	angustifolius
1559	Stenocarpus	comptonii
1560	Stenocarpus	cryptocarpus
1561	Stenocarpus	cunninghamii
1562	Stenocarpus	davallioides
1563	Stenocarpus	dumbeensis
1564	Stenocarpus	gracilis
1565	Stenocarpus	heterophyllus
1566	Stenocarpus	intermedius
1567	Stenocarpus	milnei
1568	Stenocarpus	phyllodineus
1569	Stenocarpus	reticulatus
1570	Stenocarpus	rubiginosus
1571	Stenocarpus	salignus
1572	Stenocarpus	sinuatus
1573	Stenocarpus	trinervis
1574	Stenocarpus	tremuloides
1575	Stenocarpus	umbellifer

	Genus	Species
1576	Stenocarpus	verticis
1577	Stenocarpus	villosus
1578	Stirlingia	abrotanoides
1579	Stirlingia	anethifolia
1580	Stirlingia	divaricatissima
1581	Stirlingia	latifolia
1582	Stirlingia	seselifolia
1583	Stirlingia	simplex
1584	Stirlingia	tenuifolia
1585	Strangea	linearis
1586	Strangea	stenocarpoides
1587	Strangea	cynanchicarpa
1588	Symphionema	montanum
1589	Symphionema	paludosum
1590	Synaphea	acutiloba
1591	Synaphea	aephynsa
1592	Synaphea	bifurcata
1593	Synaphea	boyaginensis
1594	Synaphea	brachyceras
1595	Synaphea	canaliculata
1596	Synaphea	cervifolia
1597	Synaphea	constricta
1598	Synaphea	cuneata
1599	Synaphea	damopsis
1600	Synaphea	decorticans
1601	Synaphea	decumbens
1602	Synaphea	diabolica
1603	Synaphea	divaricata
1604	Synaphea	drummondii
1605	Synaphea	endothrix
1606	Synaphea	favosa
1607	Synaphea	flabelliformis
1608	Synaphea	flexuosa
1609	Synaphea	floribunda
1610	Synaphea	gracillima
1611	Synaphea	grandis
1612	Synaphea	hians
1613	Synaphea	incurva
1614	Synaphea	interioris
1615	Synaphea	intricata
1616	Synaphea	lesueurensis
1617	Synaphea	macrophylla
1618	Synaphea	media
1619	Synaphea	nexosa
1620	Synaphea	obtusata
1621	Synaphea	odocoileops
1622	Synaphea	oligantha
1623	Synaphea	otiostigma
1624	Synaphea	oulopha
1625	Synaphea	pandurata
1626	Synaphea	panhesya
1627	Synaphea	parviflora
1628	Synaphea	petiolaris
1629	Synaphea	pinnata
1630	Synaphea	platyphylla
1631	Synaphea	polymorpha
1632	Synaphea	polypodioides
1633	Synaphea	preissii
1634	Synaphea	quartzitica
1635	Synaphea	rangiferops
1636	Synaphea	recurva
1637	Synaphea	reticulata
1638	Synaphea	sparsiflora
1639	Synaphea	spinulosa
1640	Synaphea	stenoloba
1641	Synaphea	tamminensis
1642	Synaphea	trinacriformis
1643	Synaphea	tripartita
1644	Synaphea	whicherensis
1645	Synaphea	xela
1646	Telopea	aspera
1647	Telopea	speciosissima
1648	Telopea	mongaensis
1649	Telopea	oreades
1650	Telopea	truncata

	Genus	Species
1651	Toronia	toru
1652	Triunia	erythrocarpa
1653	Triunia	montana
1654	Triunia	robusta
1655	Triunia	youngiana
1656	Turrillia	lutea
1657	Turrillia	ferruginea
1658	Turrillia	vitiensis
1659	Vexatorella	alpina
1660	Vexatorella	amoena
1661	Vexatorella	latebrosa
1662	Vexatorella	obtusata
1663	Virotia	angustifolia
1664	Virotia	francii
1665	Virotia	leptophylla
1666	Virotia	neurophylla
1667	Virotia	rousselii
1668	Virotia	vieillardi
1669	Xylomelum	pyriforme
1670	Xylomelum	occidentale
1671	Xylomelum	angustifolium
1672	Xylomelum	cunninghamianum
1673	Xylomelum	benthamii
1674	Xylomelum	scottianum

Synonym	Accepted Name	Source
Hakea acicularis Knight	Hakea sericea Schrad. & J.C.Wendl.	[1]
Hakea bipinnatifida	Hakea lissocarpha R.Br.	[1]
Hakea saligna (Andrews) Knight	Hakea salicifolia (Vent.) B.L.Burtt	[2]
Hakea suaveolens R.Br.	Hakea drupacea (C.F.Gaertn.) Roem. & Schult.	[2]
Hakea tenuifolia (Salisb.) Britten	Hakea sericea Schrad. & J.C.Wendl.	[1]
Hakea crassifolia Meisn.	Hakea pandanicarpa subsp. crassifolia (Meisn.) R.M.Barker	[1]
Protea mellifera	Protea repens (L.) L.	[3]
Protea barbigera Meisn.	Protea magnifica Link.	[4]
Protea latifolia R. Br.	Protea eximia (Knight) Fourc.	[3]
Protea minor (E.Phillips) Compton	Protea longifolia Andrews	[5]
Protea pulchella Andrews	Protea burchellii Stapf	[5]
Protea pulchra Rycroft	Protea burchellii Stapf	[5]
Protea subpulchella Stapf	Protea burchellii Stapf.	[4]
Protea macrocephala Thunb.	Protea coronata Lam.	[4]
Grevillea glabella R.Br.	Grevillea rosmarinifolia subsp. glabella (R.Br.) Makinson	[2]
Grevillea australis var. brevifolia Hook.f.	Grevillea australis R.Br.	[1]
Grevillea chrysodendron R.Br.	Grevillea pteridifolia Knight	[1]
Grevillea glabrata (Lindl.) Meisn.	Grevillea manglesii (Graham) Planch.	[1]
Grevillea banksii var. forsteri Guilf.	Grevillea banksii R.Br.	[1]
Grevillea diffusa subsp. evansiana (MacKee) McGill.	Grevillea evansiana MacKee	[1]
Grevillea drummondii subsp. pimeleoides (W.Fitzg.) McGill.	Grevillea pimeleoides W.Fitzg.	[1]
Grevillea linearis (Andrews) R.Br.	Grevillea linearifolia (Cav.) Druce	[1]
Grevillea macrostylis F.Muell.	Grevillea tripartita subsp. macrostylis (F.Muell.) Makinson	[1]
Grevillea ornithopoda Meisn.	Grevillea manglesii subsp. ornithopoda (Meisn.) McGill.	[1]
Grevillea gibbosa R.Br.	Grevillea glauca Knight	[1]
Grevillea juniperina f. sulphurea (A.Cunn.) I.K.Ferguson	Grevillea juniperina subsp. sulphurea (A.Cunn.) Makinson	[1]
Grevillea ericifolia R.Br.	Grevillea lanigera A.Cunn. ex R.Br.	[4]

Grevillea punicea R.Br.	Grevillea speciosa (Knight) McGill.	[1]
Grevillea williamsonii F.Muell.	Grevillea aquifolium Lindl.	[1]
Oreocallis pinnata (Maiden & Betche) Sleumer	Alloxylon pinnatum (Maiden & Betche) P.H.Weston & Crisp	[1]
Oreocallis mucronata (Willd. ex Roem. & Schult.) Sleumer	Oreocallis grandiflora (Lam.) R. Br.	[4]
Banksia australis R.Br.	Banksia marginata Cav.	[6]
Banksia patula R.Br.	Banksia marginata Cav.	[6]
Banksia collina R.Br.	Banksia spinulosa var. collina (R.Br.) A.S.George	[1]
Banksia aspleniifolia Salisb.	Banksia oblongifolia Cav.	[1]
Aulax pinifolia P.J.Bergius	Aulax cancellata (L.) Druce.	[4]
Aulax cneorifolia Knight	Aulax umbellata (Thunb.) R.Br.	[4]
Embothrium grandiflora	Oreocallis grandiflora (Lam.) R. Br.	[4]
Faurea speciosa (Welw.) Welw.	Faurea rochetiana (A. Rich.) Pic.Serm.	[7]
Gevuina bleasdalei (F.Muell.) Sleumer	Bleasdalea bleasdalei (F.Muell.) A.C.Sm. & J.E.Haas	[1]
Gevuina papuana (Diels) Sleumer	Bleasdalea papuana (Diels) Domin.	[8]
Leucadendron adscendens R. Br.	Leucadendron salignum R. Br.	[4]
Leucadendron decurrens R.Br.	Leucadendron chamelaea (Lam.) I.Williams	[4]
Leucadendron venosum R. Br.	Leucadendron daphnoides Meisn.	[4]
Leucadendron stokoei Phillips	Leucadendron microcephalum Gand. & Schinz.	[4]
Leucospermum album Bond	Leucospermum bolusii E. Phillips.	[4]
Leucospermum nutans R. Br.	Leucospermum cordifolium Fourc.	[4]
Leucospermum ellipticum R. Br.	Leucospermum cuneiforme Rourke.	[4]
Mimetes lyrigera Salisb. ex Knight nom. superf.	Mimetes cucullatus R. Br.	[4]
Roupala brasiliensis Klotzsch	Roupala montana var. paraensis (Huber) K.S. Edwards.	[4]
Roupala grossidentata Pittier	Roupala brachybotrys subsp. grossidentata (Pittier) Plana & Prance	[4]
Serruria gracilis Salisb. ex Knight	Serruria pinnata (Andr.) R.Br.	[5]
Serruria barbigera Salisb. ex Knight	Serruria phylicoides (P.J.Bergius) R.Br.	[5]

Dryandra acanthopoda A.S.George	Banksia acanthopoda (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra anatona A.S.George	Banksia anatona (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra arborea C.A.Gardner	Banksia arborea (C.A.Gardner) A.R.Mast & K.R.Thiele	[1]
Dryandra arctotidis R.Br.	Banksia arctotidis (R.Br.) A.R.Mast & K.R.Thiele	[1]
Dryandra armata R.Br.	Banksia armata (R.Br.) A.R.Mast & K.R.Thiele	[1]
Dryandra aurantia A.S.George	Banksia aurantia (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra baxteri R.Br.	Banksia biterax A.R.Mast & K.R.Thiele	[1]
Dryandra bipinnatifida R.Br.	Banksia bipinnatifida (R.Br.) A.R.Mast & K.R.Thiele	[1]
Dryandra blechnifolia R.Br.	Banksia pellaeifolia A.R.Mast & K.R.Thiele	[1]
Dryandra borealis A.S.George	Banksia borealis (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra brownii Meisn.	Banksia brunnea A.R.Mast & K.R.Thiele	[1]
Dryandra calophylla R.Br.	Banksia calophylla (R.Br.) A.R.Mast & K.R.Thiele	[1]
Dryandra carlinoides Meisn.	Banksia carlinoides (Meisn.) A.R.Mast & K.R.Thiele	[1]
Dryandra catoglypta A.S.George	Banksia catoglypta (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra cirsioides Meisn.	Banksia cirsioides (Meisn.) A.R.Mast & K.R.Thiele	[1]
Dryandra columnaris A.S.George	Banksia columnaris (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra comosa Meisn.	Banksia comosa (Meisn.) A.R.Mast & K.R.Thiele	[1]
Dryandra concinna R.Br.	Banksia concinna (R.Br.) A.R.Mast & K.R.Thiele	[1]
Dryandra conferta Benth.	Banksia densa A.R.Mast & K.R.Thiele	[1]
Dryandra corvijuga A.S.George	Banksia corvijuga (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra cuneata R.Br.	Banksia obovata A.R.Mast & K.R.Thiele	[1]
Dryandra cynaroides C.A.Gardner	Banksia cynaroides (C.A.Gardner) A.R.Mast & K.R.Thiele	[1]

Dryandra cypholoba A.S.George	Banksia cypholoba (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra drummondii Meisn.	Banksia drummondii (Meisn.) A.R.Mast & K.R.Thiele	[1]
Dryandra echinata A.S.George	Banksia echinata (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra epimicta A.S.George	Banksia epimicta (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra erythrocephala C.A.Gardner	Banksia erythrocephala (C.A.Gardner) A.R.Mast & K.R.Thiele	[1]
Dryandra falcata R.Br.	Banksia falcata (R.Br.) A.R.Mast & K.R.Thiele	[1]
Dryandra fasciculata A.S.George	Banksia fasciculata (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra ferruginea Kippist ex Meisn.	Banksia rufa A.R.Mast & K.R.Thiele	[1]
Dryandra fililoba A.S.George	Banksia fililoba (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra foliolata R.Br.	Banksia foliolata (R.Br.) A.R.Mast & K.R.Thiele	[1]
Dryandra foliosissima C.A.Gardner	Banksia foliosissima (C.A.Gardner) A.R.Mast & K.R.Thiele	[1]
Dryandra formosa R.Br.	Banksia formosa (R.Br.) A.R.Mast & K.R.Thiele	[1]
Dryandra fraseri R.Br.	Banksia fraseri (R.Br.) A.R.Mast & K.R.Thiele	[1]
Dryandra fuscobractea A.S.George	Banksia fuscobractea (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra glauca A.S.George	Banksia glaucifolia A.R.Mast & K.R.Thiele	[1]
Dryandra hewardiana Meisn.	Banksia hewardiana (Meisn.) A.R.Mast & K.R.Thiele	[1]
Dryandra hirsuta A.S.George	Banksia hirta A.R.Mast & K.R.Thiele	[1]
Dryandra horrida Meisn.	Banksia horrida (Meisn.) A.R.Mast & K.R.Thiele	[1]
Dryandra idiogenes A.S.George	Banksia idiogenes (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra insulanemorecincta A.S.George	Banksia insulanemorecincta (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra ionthocarpa A.S.George	Banksia ionthocarpa (A.S.George) A.R.Mast & K.R.Thiele	[1]

Dryandra kippistiana Meisn.	Banksia kippistiana (Meisn.) A.R.Mast & K.R.Thiele	[1]
Dryandra lepidorhiza A.S.George	Banksia lepidorhiza (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra lindleyana Meisn.	Banksia dallanneyi A.R.Mast & K.R.Thiele	[1]
Dryandra longifolia R.Br.	Banksia prolata A.R.Mast & K.R.Thiele	[1]
Dryandra meganotia A.S.George	Banksia meganotia (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra mimica A.S.George	Banksia mimica (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra montana C.A.Gardner ex A.S.George	Banksia montana (C.A.Gardner ex A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra mucronulata R.Br.	Banksia mucronulata (R.Br.) A.R.Mast & K.R.Thiele	[1]
Dryandra nana Meisn.	Banksia nana (Meisn.) A.R.Mast & K.R.Thiele	[1]
Dryandra nervosa R.Br.	Banksia alliacea A.R.Mast & K.R.Thiele	[1]
Dryandra nivea (Labill.) R.Br.	Banksia nivea Labill.	[1]
Dryandra nobilis Lindl.	Banksia nobilis (Lindl.) A.R.Mast & K.R.Thiele	[1]
Dryandra obtusa R.Br.	Banksia obtusa (R.Br.) A.R.Mast & K.R.Thiele	[1]
Dryandra octotriginta A.S.George	Banksia octotriginta (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra pallida A.S.George	Banksia pallida (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra platycarpa A.S.George	Banksia platycarpa (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra plumosa R.Br.	Banksia plumosa (R.Br.) A.R.Mast & K.R.Thiele	[1]
Dryandra polycephala Benth.	Banksia polycephala (Benth.) A.R.Mast & K.R.Thiele	[1]
Dryandra porrecta A.S.George	Banksia porrecta (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra praemorsa Meisn.	Banksia undata A.R.Mast & K.R.Thiele	[1]
Dryandra preissii Meisn.	Banksia acuminata A.R.Mast & K.R.Thiele	[1]
Dryandra prionotes A.S.George	Banksia prionophylla A.R.Mast & K.R.Thiele	[1]
Dryandra proteoides Lindl.	Banksia proteoides (Lindl.) A.R.Mast & K.R.Thiele	[1]

Dryandra pseudoplumosa A.S.George	Banksia pseudoplumosa (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra pteridifolia R.Br.	Banksia pteridifolia (R.Br.) A.R.Mast & K.R.Thiele	[1]
Dryandra pulchella Meisn.	Banksia bella A.R.Mast & K.R.Thiele	[1]
Dryandra purdieana Diels	Banksia purdieana (Diels) A.R.Mast & K.R.Thiele	[1]
Dryandra quercifolia Meisn.	Banksia heliantha A.R.Mast & K.R.Thiele	[1]
Dryandra rufistylis A.S.George	Banksia rufistylis (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra sclerophylla Meisn.	Banksia sclerophylla (Meisn.) A.R.Mast & K.R.Thiele	[1]
Dryandra seneciifolia R.Br.	Banksia seneciifolia (R.Br.) A.R.Mast & K.R.Thiele	[1]
Dryandra serra R.Br.	Banksia serra (R.Br.) A.R.Mast & K.R.Thiele	[1]
Dryandra serratuloides Meisn.	Banksia serratuloides (Meisn.) A.R.Mast & K.R.Thiele	[1]
Dryandra sessilis (Knight) Domin	Banksia sessilis (Knight) A.R.Mast & K.R.Thiele	[1]
Dryandra shanklandiorum Randall	Banksia shanklandiorum (Randall) A.R.Mast & K.R.Thiele	[1]
Dryandra shuttelworthiana Meisn.	Banksia shuttleworthiana (Meisn.) A.R.Mast & K.R.Thiele	[1]
Dryandra speciosa Meisn.	Banksia splendida A.R.Mast & K.R.Thiele	[1]
Dryandra squarrosa R.Br.	Banksia squarrosa (R.Br.) A.R.Mast & K.R.Thiele	[1]
Dryandra stenoprion Meisn.	Banksia stenoprion (Meisn.) A.R.Mast & K.R.Thiele	[1]
Dryandra stricta A.S.George	Banksia strictifolia A.R.Mast & K.R.Thiele	[1]
Dryandra stuposa Lindl.	Banksia stuposa (Lindl.) A.R.Mast & K.R.Thiele	[1]
Dryandra subpinnatifida C.A.Gardner	Banksia subpinnatifida (C.A.Gardner) A.R.Mast & K.R.Thiele	[1]
Dryandra subulata C.A.Gardner	Banksia subulata (C.A.Gardner) A.R.Mast & K.R.Thiele	[1]
Dryandra tenuifolia R.Br.	Banksia tenuis A.R.Mast & K.R.Thiele	[1]
Dryandra tortifolia Kippist ex Meisn.	Banksia tortifolia (Kippist ex Meisn.) A.R.Mast & K.R.Thiele	[1]

Dryandra tridentata Meisn.	Banksia tridentata (Meisn.) B.D.Jacks.	[1]
Dryandra trifontinalis A.S.George	Banksia trifontinalis (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra vestita Meisn.	Banksia vestita (Kippist ex Meisn.) A.R.Mast & K.R.Thiele	[1]
Dryandra viscida A.S.George	Banksia viscida (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra wonganensis A.S.George	Banksia wonganensis (A.S.George) A.R.Mast & K.R.Thiele	[1]
Dryandra xylothemelia A.S.George	Banksia xylothemelia (A.S.George) A.R.Mast & K.R.Thiele	[1]
Persoonia toru A. Cunn.	Toronia toru (A. Cunn.) L.A.S. Johnson & B.G. Briggs	[4]

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Table S3. Seventy-four literature sources and online databases that were used, in combination, to collate information on the explanatory variables.

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Table S4. Raw data of all introduced, naturalized and invasive species and the fourteen traits that were measured. See table 1 for metadata.

Genus	Species	Region of origin	Introduced status	Naturalized status	Invasive status	Height	Life form	Seed mass	Maturity	Flowering duration	Survival mechanism	Serotiny	Dispersal	Bird pollinated	Compatibility	Range size	Phytophthora	Inflorescence size	Agroforestry	Barrier	Ornamental	Forestry	Fuel	Land Rehabilitation
Adenanthos	sericeus	Australia	1			3	Shrub	NA	NA	9	1	0	Ants	1	NA	46895	VS	0	1	1	1	0	0	0
Adenanthos	argyreus	Australia	1			1	Shrub	NA	NA	3	1	0	Ants	1	NA	60520	NA	0	0	0	1	0	0	0
Adenanthos	obovatus	Australia	1			1	Shrub	NA	NA	8	0	0	NA	1	0	138769	VS	0	1	0	1	0	0	0
Adenanthos	pungens	Australia	1			3	Shrub	NA	NA	4	1	0	Ants	1	NA	13690	VS	0	0	0	0	0	0	0
Beauprea	asplenioides	New Cal	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	546	NA	0	0	0	0	0	0	0
Beauprea	balansae	New Cal	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	0	0	0
Beauprea	gracilis	New Cal	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	0	0	0
Beauprea	montana	New Cal	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	14	NA	NA	0	0	0	0	0	0
Beauprea	neglecta	New Cal	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	3059	NA	NA	0	0	0	0	0	0
Beauprea	pancheri	New Cal	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	49	NA	NA	0	0	0	0	0	0
Beauprea	spathulifolia	New Cal	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	609	NA	NA	0	0	0	0	0	0
Beaupreopsis	paniculata	New Cal	1			1.5	Shrub	NA	NA	NA	NA	NA	NA	NA	NA	109	NA	0	0	0	0	0	0	0
Bellendena	montana	Australia	1			1.8	Shrub	53.127	NA	3	NA	NA	NA	NA	NA	42071	NA	0	0	0	0	0	0	0
Aulax	umbellata	Sthn Afr	1			2.5	Shrub	32.85	1	4	1	1	Wind	0	0	12861	NA	NA	0	0	0	0	0	0
Aulax	cancellata	Sthn Afr	1			2.5	Shrub	37	2	4	1	1	Wind	0	0	29185	VS	0	0	0	0	0	0	0
Aulax	pallasia	Sthn Afr	1			3	Shrub	10.5	2	4	0	1	Wind	0	0	23127	NA	0	0	0	0	0	0	0
Protea	acaulos	Sthn Afr	1			0.3	Shrub	NA	1	6	0	1	Wind	1	NA	40477	NA	0	1	0	0	0	0	0
Protea	acuminata	Sthn Afr	1			2	Shrub	10.8	1	4	1	1	Wind	1	NA	10089	NA	0	1	0	0	0	0	0
Protea	amplexicaulis	Sthn Afr	1			0.4	Shrub	12.79	1	4	1	1	Wind	0	NA	10452	NA	0	1	0	0	0	0	0
Protea	cynaroides	Sthn Afr	1	1		2	Shrub	23.48	1	12	0	1	Wind	1	NA	140573	Res	1	1	0	0	0	0	0
Protea	susannae	Sthn Afr	1			3	Shrub	22.74	1	6	1	1	Wind	1	0	28791	NA	1	1	0	0	0	0	0
Protea	coronata	Sthn Afr	1			3	Shrub	35.15	1	6	1	1	Wind	1	NA	64231	NA	1	1	0	0	0	0	0
Protea	subvestita	Sthn Afr	1	1		5	Shrub	6.92	1	7	1	1	Wind	1	NA	112722	NA	0	1	0	0	0	0	0
Protea	aristata	Sthn Afr	1			2.5	Shrub	NA	5	5	1	1	Wind	1	NA	420	NA	1	1	0	0	0	0	0
Protea	aurea	Sthn Afr	1			5	Shrub	NA	1	12	1	1	Wind	1	0	35538	NA	1	1	0	0	0	0	0
Protea	aurea subsp. potbergensis	Sthn Afr	1			5	Shrub	NA	6	4	1	1	Wind	1	NA	19	NA	1	1	0	0	0	0	0
Protea	burchellii	Sthn Afr	1			2	Shrub	13.87	3	3	1	1	Wind	1	NA	12176	NA	1	1	0	0	0	0	0
Protea	caffra	Sthn Afr	1			5	Shrub	NA	1	4	0	0	Wind	1	NA	NA	Res	0	1	0	0	0	0	0
Protea	canaliculata	Sthn Afr	1			1.2	Shrub	NA	1	4	1	1	Wind	1	NA	7596	NA	0	1	0	0	0	0	0
Protea	compacta	Sthn Afr	1			3.5	Shrub	90.9	1	6	1	1	Wind	1	1	10080	Res	1	1	0	0	0	0	0
Protea	cordata	Sthn Afr	1			0.5	Shrub	18.2	2	2	1	1	Wind	1	NA	15068	NA	0	1	0	0	0	0	0
Protea	decurrens	Sthn Afr	1			0.6	Shrub	NA	3	4	1	1	Wind	0	NA	6248	NA	0	1	0	0	0	0	0
Protea	denticulata	Sthn Afr	1			1	Shrub	NA	1	3	0	1	Wind	1	NA	139	NA	0	1	0	0	0	0	0
Protea	dracomontana	Sthn Afr	1			1.5	Shrub	NA	1	3	0	0	Wind	1	NA	18023	NA	0	1	0	0	0	0	0
Protea	effusa	Sthn Afr	1			1.5	Shrub	NA	1	5	0	1	NA	0	NA	5719	NA	1	1	0	0	0	0	0
Protea	eximia	Sthn Afr	1			5	Shrub	36.26	1	6	1	1	Wind	1	0	88544	Res	1	1	0	0	0	0	0
Protea	gaguedi	Sthn Afr	1			3	Shrub	NA	1	8	1	0	Wind	1	NA	792376	NA	1	1	0	0	0	0	0
Protea	grandiceps	Sthn Afr	1			2	Shrub	NA	1	5	1	1	Wind	1	NA	32935	NA	1	1	0	0	0	0	0
Protea	holosericea	Sthn Afr	1			1.2	Shrub	NA	6	2	1	1	Wind	1	NA	9	NA	0	1	0	0	0	0	0
Protea	lacticolor	Sthn Afr	1			6	Shrub	NA	3	5	1	1	Wind	1	0	2294	NA	0	1	0	0	0	0	0
Protea	laevis	Sthn Afr	1			0.2	Shrub	13.35	1	6	1	1	Wind	1	NA	5296	NA	0	1	0	0	0	0	0

Protea	lanceolata	Sthn Afr	1			4	Shrub	16.27	4	7	1	1	Wind	1	NA	3709	Sus	0	1	0	0	0	0
Protea	laurifolia	Sthn Afr	1			5	Shrub	15.81	1	8	1	1	Wind	1	0	146988	Res	1	1	0	0	0	0
Protea	lepidocarpodendron	Sthn Afr	1			3	Shrub	34.8	1	5	1	1	Wind	1	NA	3566	NA	1	1	0	0	0	0
Protea	longifolia	Sthn Afr	1			1.5	Shrub	43.59	1	5	1	1	Wind	1	0	7169	Sus	1	1	0	0	0	0
Protea	lorifolia	Sthn Afr	1			3	Shrub	16.08	1	7	1	1	Wind	1	NA	60873	NA	1	1	0	0	0	0
Protea	magnifica	Sthn Afr	1			2.5	Shrub	118.17	1	8	1	1	Wind	1	NA	45317	Sus	1	1	0	0	0	0
Protea	mundii	Sthn Afr	1			8	Shrub	18.42	1	9	1	1	Wind	1	0	36336	NA	0	1	0	0	0	0
Protea	nana	Sthn Afr	1			1.3	Shrub	8.37	1	4	1	1	Wind	0	NA	1073	NA	0	1	0	0	0	0
Protea	neriifolia	Sthn Afr	1			3	Shrub	19.13	1	10	1	1	Wind	1	0	94843	Res	1	1	0	0	0	0
Protea	nitida	Sthn Afr	1			5	Tree	47.4	1	12	0	1	Wind	1	NA	129063	Res	1	1	0	0	0	0
Protea	obtusifolia	Sthn Afr	1			4	Shrub	13.94	1	6	1	1	Wind	1	0	13162	Res	1	1	0	0	0	0
Protea	pudens	Sthn Afr	1			0.4	Shrub	NA	5	5	1	1	Wind	1	NA	66	NA	0	1	0	0	0	0
Protea	pityphylla	Sthn Afr	1			1	Shrub	6.34	9	5	1	1	Wind	NA	NA	750	NA	0	1	0	0	0	0
Protea	punctata	Sthn Afr	1			4	Shrub	11.76	1	7	1	1	Wind	1	NA	71846	NA	0	1	0	0	0	0
Protea	recondita	Sthn Afr	1			1	Shrub	9.3	2	5	1	1	Wind	1	NA	3956	NA	0	1	0	0	0	0
Protea	repens	Sthn Afr	1	1		4.5	Shrub	67.9	1	12	1	1	Wind	1	0	183184	Res	1	1	0	0	0	0
Protea	roupelliae	Sthn Afr	1			8	Tree	14.42	1	12	1	1	Wind	1	NA	329064	NA	1	1	0	0	0	0
Protea	rubropilosa	Sthn Afr	1			8	Tree	NA	1	4	1	0	Wind	1	NA	10467	NA	0	1	0	0	0	0
Protea	scabra	Sthn Afr	1			0.2	Shrub	35.31	2	7	0	1	Wind	0	NA	7671	NA	0	1	0	0	0	0
Protea	scabriuscula	Sthn Afr	1			0.5	Shrub	NA	2	4	0	1	Wind	NA	NA	1876	NA	0	1	0	0	0	0
Protea	scolymocephala	Sthn Afr	1			1.5	Shrub	NA	1	5	1	1	Wind	0	NA	90476	NA	0	1	0	0	0	0
Protea	simplex	Sthn Afr	1			1	Shrub	NA	1	2	0	0	Wind	1	NA	254669	NA	0	1	0	0	0	0
Protea	speciosa	Sthn Afr	1			1.2	Shrub	44.97	1	8	0	1	Wind	1	NA	18923	NA	1	1	0	0	0	0
Protea	stokoei	Sthn Afr	1			2	Shrub	NA	8	6	1	1	Wind	1	NA	496	NA	1	1	0	0	0	0
Protea	venusta	Sthn Afr	1			0.7	Shrub	NA	2	3	1	1	Wind	1	NA	2423	NA	1	1	0	0	0	0
Protea	welwitschii	Sthn Afr /Afr	1			1.5	Shrub	17.4	1	6	0	0	Wind	1	NA	1392382	NA	0	1	0	0	0	0
Faurea	rochetiana	Sthn Afr /Afr	1			7	Tree	NA	1	7	0	0	Wind	0	NA	420823	NA	1	0	0	0	1	0
Faurea	saligna	Sthn Afr	1			10	Tree	NA	1	7	0	0	Wind	0	NA	1357041	NA	1	0	1	1	1	1
Isopogon	anemonifolius	Australia	1			2	Shrub	4.56	NA	6	0	1	Unspec	0	NA	155081	VS	0	1	0	1	0	0
Isopogon	anethifolius	Australia	1			2	Shrub	3.4	NA	3	0	1	Unspec	0	NA	35320	NA	0	1	1	0	0	0
Isopogon	dawsonii	Australia	1			5	Shrub	2.74	NA	3	1	1	Unspec	0	NA	17820	NA	0	1	0	0	0	0
Isopogon	formosus	Australia	1			2	Shrub	NA	NA	5	NA	1	Unspec	0	NA	238493	VS	0	1	0	0	0	0
Isopogon	dubius	Australia	1			1.2	Shrub	NA	NA	3	NA	1	Unspec	0	NA	42662	NA	0	1	0	1	0	0
Isopogon	petiolaris	Australia	1			1	Shrub	3.77	NA	5	NA	1	Unspec	0	NA	196457	NA	0	0	0	1	0	0
Leucadendron	album	Sthn Afr	1			2	Shrub	18.99	1	1	1	1	Wind	0	0	17324	NA	0	1	0	1	0	0
Leucadendron	argenteum	Sthn Afr	1	1		10	Tree	252.01	2	1	1	1	Wind	0	0	1303	VS	0	1	0	1	0	0
Leucadendron	arcuatum	Sthn Afr	1			1.3	Shrub	NA	2	2	0	0	Mammals	0	0	5494	NA	0	1	0	0	0	0
Leucadendron	brunioides	Sthn Afr	1			2	Shrub	19.34	2	2	0	0	Wind	0	0	41672	NA	0	1	0	0	0	0
Leucadendron	chamelaea	Sthn Afr	1			2.3	Shrub	NA	1	1	1	0	Unspec	0	0	1510	NA	0	1	0	0	0	0
Leucadendron	comosum	Sthn Afr	1			1.7	Shrub	NA	2	2	1	1	Wind	0	0	21266	NA	0	1	0	0	0	0
Leucadendron	conicum	Sthn Afr	1			6	Shrub	NA	3	2	1	1	Wind	0	0	7129	NA	0	1	0	0	0	0

Leucadendron	coniferum	Sthn Afr	1			4	Shrub	10.47	2	2	1	1	Wind	0	0	13056	VS	0	1	0	0	0	0
Leucadendron	cryptocephalum	Sthn Afr	1			1	Shrub	NA	8	3	1	1	Wind	NA	0	138	NA	0	1	0	0	0	0
Leucadendron	daphnoides	Sthn Afr	1			1.5	Shrub	200	2	3	1	0	Mammals	0	0	5427	NA	0	1	0	0	0	0
Leucadendron	discolor	Sthn Afr	1			2	Shrub	7.12	6	1	1	1	Unspec	0	0	2125	NA	0	1	0	0	0	0
Leucadendron	dregei	Sthn Afr	1			0.6	Shrub	14	1	2	1	1	Wind	0	0	3665	NA	0	1	0	0	0	0
Leucadendron	dubium	Sthn Afr	1			1.3	Shrub	61.05	3	2	1	0	Mammals	0	0	700	NA	0	1	0	0	0	0
Leucadendron	elimense	Sthn Afr	1			1.5	Shrub	34.51	2	3	1	0	Unspec	0	0	827	NA	0	1	0	0	0	0
Leucadendron	ericifolium	Sthn Afr	1	1		1.2	Shrub	NA	5	1	1	0	Ants	0	0	3093	NA	0	1	0	0	0	0
Leucadendron	eucalyptifolium	Sthn Afr	1			5	Shrub	8.96	1	4	1	1	Wind	0	0	44525	Res	0	1	0	0	0	0
Leucadendron	flexuosum	Sthn Afr	1			2.5	Shrub	NA	1	2	0	1	Wind	0	0	148	NA	0	1	0	0	0	0
Leucadendron	floridum	Sthn Afr	1			2	Shrub	6.51	7	2	1	1	Unspec	0	0	146	NA	0	1	0	0	0	0
Leucadendron	galpinii	Sthn Afr	1			3	Shrub	18.5	3	2	1	1	Unspec	0	0	4401	VS	0	1	0	0	0	0
Leucadendron	gandogeri	Sthn Afr	1			1.6	Shrub	23	1	2	1	1	Wind	0	0	4097	Res	0	1	0	0	0	0
Leucadendron	glaberrimum	Sthn Afr	1			1.3	Shrub	108.38	1	3	1	0	Mammals	0	0	3526	NA	0	1	0	0	0	0
Leucadendron	grandiflorum	Sthn Afr	1			2	NA	NA	1	2	1	NA	NA	0	0	NA	NA	NA	0	0	0	0	0
Leucadendron	gydoense	Sthn Afr	1			1.3	Shrub	NA	9	1	1	0	NA	NA	0	492	NA	0	1	0	0	0	0
Leucadendron	lanigerum	Sthn Afr	1			1.5	Shrub	5.45	2	3	0	1	Wind	0	0	7000	NA	0	1	0	0	0	0
Leucadendron	laureolum	Sthn Afr	1			2	Shrub	25.6	1	1	1	1	Wind	0	0	20586	Sus	0	1	0	0	0	0
Leucadendron	laxum	Sthn Afr	1			1.5	Shrub	504.68	6	2	1	0	NA	0	0	1221	NA	0	1	0	0	0	0
Leucadendron	levisanus	Sthn Afr	1			2	Shrub	5.48	1	1	1	1	Unspec	0	0	657	NA	0	1	0	0	0	0
Leucadendron	linifolium	Sthn Afr	1			2	Shrub	12.8	1	2	1	1	Unspec	0	0	12006	Sus	0	1	0	0	0	0
Leucadendron	loeriense	Sthn Afr	1			2.5	Shrub	NA	1	2	1	1	Unspec	0	0	7312	NA	0	1	0	0	0	0
Leucadendron	loranthifolium	Sthn Afr	1			2	Shrub	NA	1	3	1	0	Mammals	0	0	12169	NA	0	1	0	0	0	0
Leucadendron	macowanii	Sthn Afr	1			2.3	Shrub	NA	3	3	1	1	Unspec	0	0	4	NA	0	1	0	0	0	0
Leucadendron	meridianum	Sthn Afr	1			2	Shrub	32.69	1	1	1	1	Wind	0	0	25592	NA	0	1	0	0	0	0
Leucadendron	microcephalum	Sthn Afr	1			1.5	Shrub	27.68	1	1	1	1	Wind	0	0	4780	NA	0	1	0	0	0	0
Leucadendron	modestum	Sthn Afr	1			0.6	Shrub	20.17	1	1	1	1	Wind	0	0	4172	NA	0	1	0	0	0	0
Leucadendron	muirii	Sthn Afr	1			2	Shrub	4.68	1	2	1	1	Wind	0	0	3855	NA	0	1	0	0	0	0
Leucadendron	nervosum	Sthn Afr	1			1.5	Shrub	NA	6	1	1	1	Wind	1	0	1152	Res	0	1	0	0	0	0
Leucadendron	nobile	Sthn Afr	1			4	Shrub	5.86	1	6	1	1	Wind	0	0	6557	NA	0	1	0	0	0	0
Leucadendron	orientale	Sthn Afr	1			1.3	Shrub	NA	5	2	1	0	Mammals	0	0	570	VS	0	1	0	0	0	0
Leucadendron	platyspermum	Sthn Afr	1			1.7	Shrub	97.04	1	1	1	1	Wind	0	0	4255	NA	0	1	0	0	0	0
Leucadendron	procerum	Sthn Afr	1			3	Shrub	12.65	2	1	1	1	Wind	0	0	5734	VS	0	1	0	0	0	0
Leucadendron	pubescens	Sthn Afr	1			2.5	Shrub	135.53	1	5	1	0	Mammals	0	0	34644	NA	0	1	0	0	0	0
Leucadendron	rourkei	Sthn Afr	1			5	Shrub	5.76	2	2	1	1	Unspec	0	0	2230	NA	0	1	0	0	0	0
Leucadendron	rubrum	Sthn Afr	1	1		2.5	Shrub	23.94	1	2	1	1	Wind	1	0	114751	VS	0	1	0	0	0	0
Leucadendron	salicifolium	Sthn Afr	1			3	Shrub	19	1	3	1	1	Unspec	0	0	32268	VS	0	1	0	0	0	0
Leucadendron	salignum	Sthn Afr	1			2	Shrub	8.3	1	8	1	0	Wind	0	0	185873	VS	0	1	0	0	0	0
Leucadendron	sessile	Sthn Afr	1			1.5	Shrub	200	2	2	1	0	Mammals	0	0	3454	NA	0	1	0	0	0	0
Leucadendron	spissifolium	Sthn Afr	1			1.3	Shrub	12.24	1	3	0	1	Wind	0	0	43416	NA	0	1	0	0	0	0
Leucadendron	stelligerum	Sthn Afr	1			1.3	Shrub	4.83	4	2	1	1	NA	0	0	109	NA	0	1	0	0	0	0

Leucadendron	strobilinum	Sthn Afr	1			2.6	Shrub	NA	1	2	1	1	Wind	0	0	134	NA	0	1	0	0	0	0
Leucadendron	teretifolium	Sthn Afr	1			1	Shrub	4.84	1	2	1	1	Wind	0	0	27976	NA	0	1	0	0	0	0
Leucadendron	thymifolium	Sthn Afr	1			2	Shrub	29.53	5	2	1	0	Unspec	0	0	263	NA	0	1	0	0	0	0
Leucadendron	tinctum	Sthn Afr	1			1.3	Shrub	229	3	1	1	0	Mammals	0	0	46870	NA	0	1	0	0	0	0
Leucadendron	uliginosum	Sthn Afr	1			2.3	Shrub	4.66	3	1	1	1	Unspec	1	0	2668	Res	0	1	0	0	0	0
Leucadendron	xanthoconus	Sthn Afr	1			2	Shrub	10.85	1	1	1	1	Wind	0	0	14947	NA	0	1	0	0	0	0
Leucospermum	bolusii	Sthn Afr	1			1.5	Shrub	NA	2	4	1	0	Ants	0	NA	29	NA	0	1	0	0	0	0
Leucospermum	catherinae	Sthn Afr	1			3	Shrub	81.2	1	4	1	0	Ants	1	NA	4162	NA	1	1	0	0	0	0
Leucospermum	conocarpodendron	Sthn Afr	1			5	Tree	100	4	5	1	0	Ants	1	NA	51	Sus	0	1	0	1	0	1
Leucospermum	cordifolium	Sthn Afr	1			1.5	Shrub	100	1	6	1	0	Ants	1	1	7323	VS	1	1	0	1	0	0
Leucospermum	cuneiforme	Sthn Afr	1			3	Shrub	NA	1	12	0	0	Ants	1	1	76362	VS	0	1	0	1	0	0
Leucospermum	erubescens	Sthn Afr	1			2	Shrub	NA	4	6	1	0	Ants	1	0	642	NA	0	1	0	0	0	0
Leucospermum	formosum	Sthn Afr	1			3	Shrub	NA	4	2	1	0	Ants	1	NA	5628	Res	1	1	0	1	0	0
Leucospermum	glabrum	Sthn Afr	1			2.5	Shrub	108	8	3	1	0	Ants	1	NA	1323	Sus	0	1	0	1	0	0
Leucospermum	grandiflorum	Sthn Afr	1			2.5	Shrub	NA	3	6	1	0	Ants	1	NA	525	NA	1	1	0	0	0	0
Leucospermum	gueinzii	Sthn Afr	1			3	Shrub	NA	2	5	1	0	Ants	1	NA	498	NA	1	1	0	0	0	0
Leucospermum	hypophyllocarpodendron	Sthn Afr	1			0.2	Shrub	2.02	2	6	1	0	Ants	0	NA	10949	NA	0	1	0	1	0	0
Leucospermum	lineare	Sthn Afr	1			2	Shrub	NA	3	7	1	0	Ants	1	NA	916	NA	0	1	0	1	0	0
Leucospermum	muirii	Sthn Afr	1			1.5	Shrub	24.13	3	4	1	0	Ants	1	NA	265	NA	0	1	0	1	0	0
Leucospermum	mundii	Sthn Afr	1			1	Shrub	NA	5	5	1	0	Ants	1	1	531	NA	0	1	0	0	0	0
Leucospermum	oleifolium	Sthn Afr	1			1	Shrub	NA	2	6	1	0	Ants	1	1	6120	NA	0	1	0	1	0	0
Leucospermum	patersonii	Sthn Afr	1			4	Tree	NA	2	5	1	0	Ants	1	NA	822	VS	0	1	0	1	0	0
Leucospermum	praecox	Sthn Afr	1			3	Shrub	76.92	3	6	1	0	Ants	1	NA	2127	NA	0	1	0	1	0	0
Leucospermum	prostratum	Sthn Afr	1			NA	Shrub	24.3	1	6	0	0	Ants	0	NA	2762	VS	0	1	0	0	0	0
Leucospermum	reflexum	Sthn Afr	1			4	Shrub	NA	2	5	1	0	Ants	1	1	3429	Sus	1	1	0	1	0	0
Leucospermum	rodolentum	Sthn Afr	1			3	Shrub	64.65	3	4	1	0	Ants	0	NA	24532	NA	0	1	0	0	0	0
Leucospermum	saxosum	Sthn Afr	1			2	Shrub	NA	NA	12	0	0	Ants	1	NA	22872	NA	0	1	0	1	0	0
Leucospermum	tottum	Sthn Afr	1			1.5	Shrub	NA	5	5	1	0	Ants	1	NA	5106	NA	1	1	0	1	0	0
Leucospermum	vestitum	Sthn Afr	1			2.5	Shrub	NA	4	7	1	0	Ants	1	NA	7949	NA	0	1	0	1	0	0
Paranomus	bolusii	Sthn Afr	1			1	Shrub	NA	3	6	1	0	Ants	0	NA	1292	NA	0	0	0	0	0	0
Paranomus	reflexus	Sthn Afr	1			1.5	Shrub	NA	7	3	1	0	Ants	0	NA	664	Sus	1	1	0	1	0	0
Paranomus	bracteolaris	Sthn Afr	1			2	Shrub	30.43	1	3	1	0	Ants	0	NA	6444	NA	0	1	0	1	0	0
Paranomus	spicatus	Sthn Afr	1			1	Shrub	NA	5	3	1	0	Ants	0	NA	159	NA	0	1	0	1	0	0
Knightia	excelsa	Sthn Afr	1			30	Tree	29	NA	2	NA	NA	Wind	0	NA	78812	NA	1	0	0	1	1	0
Eucarpha	deplanchei	New Cal	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	0	0
Roupala	brachybotrys subsp. grossidentata	America	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	0	0
Roupala	longepetiolata	America	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	0	0
Roupala	macrophylla	America	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	0	0
Roupala	montana	America	1			NA	NA	47	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	0	0
Roupala	montana var. paraensis	America	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	0	0

Roupala	pseudocordata	America	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	0	0
Serruria	acrocarpa	Sthn Afr	1			0.5	Shrub	3.5	1	8	0	0	Ants	0	NA	3682	NA	0	1	0	0	0	0
Serruria	adscendens	Sthn Afr	1			1	Shrub	NA	3	4	1	0	Ants	0	NA	661	NA	0	1	0	0	0	0
Serruria	aitonii	Sthn Afr	1			1	Shrub	7.26	1	5	1	0	Ants	0	NA	7063	NA	0	1	0	0	0	0
Serruria	aemula	Sthn Afr	1			0.5	Shrub	NA	1	4	1	0	Ants	0	NA	NA	NA	0	1	0	1	0	0
Serruria	elongata	Sthn Afr	1			1.5	Shrub	2.7	1	4	1	0	Ants	0	NA	6927	NA	1	1	0	0	0	0
Serruria	florida	Sthn Afr	1			2	Shrub	NA	2	4	1	0	Ants	0	NA	2	VS	0	1	0	1	0	0
Serruria	fucifolia	Sthn Afr	1			1.5	Shrub	NA	3	4	1	0	Ants	0	NA	5077	NA	0	0	0	1	0	0
Serruria	glomerata	Sthn Afr	1			0.4	Shrub	5.39	1	3	1	0	Ants	0	NA	326	NA	0	1	0	0	0	0
Serruria	linearis	Sthn Afr	1			0.8	Shrub	NA	2	4	0	0	Ants	0	NA	167	NA	0	1	0	0	0	0
Serruria	pedunculata	Sthn Afr	1			1	Shrub	21.37	2	5	1	0	Ants	0	NA	1344	NA	0	1	0	0	0	0
Serruria	phylicoides	Sthn Afr	1			1	Shrub	12	2	4	1	0	Ants	0	NA	3275	NA	0	1	0	0	0	0
Serruria	pinnata	Sthn Afr	1			0.1	Shrub	NA	NA	4	0	0	Ants	0	NA	2	NA	NA	0	0	0	0	0
Serruria	rosea	Sthn Afr	1			1.5	Shrub	18.58	4	3	1	0	Ants	0	NA	234	NA	0	0	0	1	0	0
Orites	myrtoidea	America	1			2	Shrub	7.29	NA	2	NA	NA	Wind	NA	NA	113925	NA	0	0	0	1	0	0
Banksia	aemula	Australia	1	1		8	Shrub	84	NA	4	0	1	Wind	1	NA	378097	Res	1	0	1	1	0	0
Banksia	ashbyi	Australia	1			8	Shrub	16.72	NA	3	NA	1	Wind	1	NA	118841	VS	1	1	0	1	0	0
Banksia	attenuata	Australia	1			4	Shrub	104	3	5	0	1	Wind	0	0	298922	VS	1	1	1	0	0	0
Banksia	baxteri	Australia	1			4	Shrub	40.5	2	6	1	1	Wind	1	1	19419	VS	0	1	1	0	0	0
Banksia	burdettii	Australia	1			4	Shrub	103.4	NA	5	1	1	Wind	1	NA	6609	VS	1	1	0	0	0	0
Banksia	caleyi	Australia	1	1		2	Shrub	NA	5	3	1	1	Wind	0	NA	18831	Sus	0	0	0	1	0	0
Banksia	canei	Australia	1	1		3	Shrub	8.75	NA	6	1	1	Wind	NA	NA	42864	NA	1	0	0	1	0	0
Banksia	coccinea	Australia	1			8	Tree	12.9	5	8	1	1	Wind	1	1	88654	VS	0	1	0	1	0	0
Banksia	conferta	Australia	1			4	Shrub	NA	NA	4	1	1	Wind	0	NA	96383	NA	1	0	0	1	0	0
Banksia	dryandroides	Australia	1			1	Shrub	NA	NA	4	1	1	Wind	NA	NA	8368	VS	0	0	1	1	0	0
Banksia	ericifolia	Australia	1		1	6	Shrub	20	5	5	1	1	Wind	1	1	101066	Res	1	1	1	1	0	0
Banksia	ericifolia var. macrantha	Australia	1			6	Shrub	NA	NA	5	1	1	Wind	1	NA	15238	NA	1	1	0	1	0	0
Banksia	grandis	Australia	1	1		10	Tree	NA	3	4	0	1	Wind	1	0	97008	VS	1	0	0	1	0	0
Banksia	hookeriana	Australia	1			3	Shrub	53	4	7	1	1	Wind	1	1	8652	VS	1	1	0	1	0	0
Banksia	integrifolia	Australia	1		1	10	Tree	13.67	NA	7	0	1	Wind	1	1	684608	Res	1	0	0	1	0	0
Banksia	marginata	Australia	1			12	Tree	7.88	NA	6	NA	1	Wind	1	NA	1114806	Sus	1	0	1	1	0	0
Banksia	media	Australia	1			10	Shrub	39.65	NA	6	1	1	Wind	1	1	107967	Sus	1	0	1	1	0	0
Banksia	menziesii	Australia	1			3	Shrub	87.3	NA	7	0	1	Wind	1	0	248037	VS	1	1	0	0	0	0
Banksia	nutans	Australia	1			1	Shrub	NA	NA	4	1	1	Wind	0	1	237469	VS	0	0	0	1	0	0
Banksia	oblongifolia	Australia	1			3	Shrub	17.9	NA	4	0	1	Wind	1	NA	399202	Res	1	0	0	1	0	0
Banksia	occidentalis	Australia	1			7	Shrub	9.5	NA	4	1	1	Wind	1	NA	158926	VS	1	0	1	1	0	0
Banksia	ornata	Australia	1			3	Shrub	27.14	NA	4	1	1	Wind	1	NA	136977	VS	1	0	1	1	0	0
Banksia	paludosa	Australia	1	1		2	Shrub	NA	NA	4	0	1	Wind	1	1	42829	Res	1	0	0	1	0	0
Banksia	praemorsa	Australia	1			4	Shrub	NA	NA	4	1	1	Wind	1	NA	4612	VS	1	0	0	1	0	0
Banksia	pilostylis	Australia	1			4	Shrub	58.97	2	4	1	1	Wind	1	NA	16991	Sus	1	0	0	1	0	0
Banksia	prionotes	Australia	1			10	Shrub	24	NA	7	1	1	Wind	1	1	335755	VS	1	1	0	1	0	0

Banksia	quercifolia	Australia	1			3	Shrub	NA	NA	4	1	1	Wind	1	NA	21862	VS	1	0	1	1	0	0
Banksia	robur	Australia	1	1		3	Shrub	23.76	3	7	0	1	Wind	1	NA	735670	Res	1	0	0	1	0	0
Banksia	saxicola	Australia	1			3	Shrub	10.8	NA	3	1	1	Wind	1	NA	54507	VS	0	0	0	1	0	0
Banksia	sceptrum	Australia	1			5	Shrub	NA	NA	2	1	1	Wind	1	NA	25538	VS	1	1	0	1	0	0
Banksia	serrata	Australia	1	1		16	Tree	56.03	9	6	0	1	Wind	1	1	664355	Res	1	0	0	1	0	0
Banksia	speciosa	Australia	1			8	Shrub	121.2	NA	12	1	1	Wind	1	1	240224	VS	1	1	1	0	0	0
Banksia	sphaerocarpa	Australia	1			2	Shrub	NA	NA	7	0	1	Wind	1	NA	224992	VS	0	0	1	1	0	0
Banksia	spinulosa	Australia	1	1		3	Shrub	13.45	NA	4	0	1	Wind	1	0	1469514	NA	1	0	0	1	0	0
Banksia	spinulosa var. collina	Australia	1	1		3	Shrub	10.9	NA	4	0	1	Wind	1	NA	775056	Res	1	0	0	1	0	0
Banksia	spinulosa var. cunninghamii	Australia	1			6	Shrub	NA	NA	4	1	1	Wind	1	NA	371655	VS	1	0	0	1	0	0
Banksia	verticillata	Australia	1			5	Shrub	NA	NA	4	1	1	Wind	1	NA	26046	VS	1	0	1	0	0	0
Banksia	victoriae	Australia	1			7	Shrub	NA	NA	2	1	1	Wind	1	NA	13631	VS	1	1	0	1	0	0
Banksia	violacea	Australia	1			1.5	Shrub	12.27	NA	4	1	1	Wind	1	NA	78063	VS	0	0	0	1	0	0
Banksia	armata	Australia	1			1.5	Shrub	8.65	NA	3	0	0	Wind	1	NA	274883	VS	0	1	0	1	0	0
Banksia	calophylla	Australia	1			NA	Shrub	NA	NA	2	0	NA	Wind	1	NA	8477	VS	0	0	0	1	0	0
Banksia	formosa	Australia	1	1		4	Shrub	NA	NA	4	1	0	Wind	1	1	68533	Sus	1	1	0	1	0	0
Banksia	dallanneyi	Australia	1			3	Shrub	NA	NA	4	0	NA	Wind	1	NA	435315	VS	0	0	0	1	0	0
Banksia	nobilis	Australia	1			4	Shrub	NA	NA	4	1	NA	Wind	1	NA	61628	NA	NA	1	0	1	0	0
Banksia	undata	Australia	1	1		3	Shrub	NA	NA	4	1	1	Wind	1	NA	8503	NA	0	1	0	1	0	0
Banksia	heliantha	Australia	1			3	Shrub	14.65	NA	4	1	0	Wind	1	1	10369	VS	0	1	0	1	0	0
Banksia	proteoides	Australia	1			2	Shrub	NA	NA	3	1	NA	Wind	1	NA	15176	NA	1	0	0	1	0	0
Banksia	stuposa	Australia	1			3	Shrub	NA	NA	3	1	NA	Wind	1	NA	28369	NA	0	1	0	1	0	0
Banksia	insulanemorecincta	Australia	1			1	Shrub	NA	NA	4	1	NA	Wind	1	NA	NA	NA	0	0	0	0	0	0
Embothrium	coccineum	America	1	1		1.2	Shrub	15.6	NA	3	NA	NA	Wind	1	0	NA	NA	0	1	0	1	0	0
Gevuina	avellana	America	1			20	Tree	NA	NA	5	NA	0	Mammals	0	NA	NA	NA	NA	1	0	1	0	0
Telopea	mongaensis	Australia	1			6	Shrub	38.21	NA	3	0	0	Wind	1	NA	9980	NA	1	0	0	1	0	0
Telopea	truncata	Australia	1			3	Shrub	29.71	NA	4	0	0	Wind	1	NA	61079	NA	0	0	0	1	0	0
Telopea	speciosissima	Australia	1	1		3	Shrub	54.26	5	4	0	0	Wind	1	0	63869	NA	1	1	0	1	0	0
Telopea	oreades	Australia	1	1		12	Shrub	35.26	NA	3	0	0	Wind	1	NA	91158	NA	0	0	0	1	0	0
Stenocarpus	cunninghamii	Australia	1	1		10	Tree	NA	NA	3	0	0	Wind	NA	NA	98122	NA	NA	0	0	1	0	0
Stenocarpus	gracilis	New Cal	1			NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	0	0	0	0	0
Stenocarpus	salignus	Australia	1	1		30	Tree	NA	NA	4	0	0	Wind	1	NA	973828	NA	NA	0	0	1	1	0
Stenocarpus	sinuatus	Australia	1	1		30	Tree	57	7	4	NA	0	Wind	1	NA	577296	Res	1	0	0	1	0	0
Stenocarpus	trinervis	New Cal	1			NA	NA	NA	NA	NA	NA	0	NA	NA	NA	8721	NA	NA	0	0	0	0	0
Stenocarpus	umbellifer	New Cal	1			NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	0	0	0	0	0
Hakea	baxteri	Australia	1			5	Shrub	39.9	NA	2	1	1	Wind	NA	NA	36777	Sus	0	0	0	1	0	0
Hakea	bucculenta	Australia	1	1		4	Shrub	12.9	NA	6	1	1	Wind	1	NA	39478	NA	1	0	1	1	0	0
Hakea	clavata	Australia	1			2	Shrub	12.1	NA	10	0	0	Wind	NA	NA	133250	NA	0	0	0	1	0	0
Hakea	costata	Australia	1	1		1.5	Shrub	7	NA	4	1	1	Wind	0	NA	43717	NA	0	0	0	1	0	0
Hakea	cristata	Australia	1	1		2	Shrub	85.2	NA	4	0	1	Wind	0	1	3216	NA	0	0	1	1	0	0

Hakea	cucullata	Australia	1	1		4	Shrub	29	NA	7	1	1	Wind	1	NA	14428	Sus	0	1	0	1	0	0
Hakea	cyclocarpa	Australia	1			2.5	Shrub	88.1	NA	3	0	1	Wind	NA	NA	48744	NA	0	0	0	1	0	0
Hakea	dactyloides	Australia	1			4.5	Shrub	23.17	4	2	1	1	Wind	0	NA	362403	Sus	0	1	0	1	0	0
Hakea	decurrens	Australia	1	1		2.4	Shrub	25.2	NA	5	0	1	Wind	NA	NA	610361	Sus	0	0	1	0	0	0
Hakea	drupacea	Australia	1		1	4	Shrub	17.1	2	4	1	1	Wind	0	NA	79030	NA	0	0	1	0	0	0
Hakea	elliptica	Australia	1	1		4	Shrub	18.4	NA	1	1	1	Wind	NA	NA	41694	Sus	0	1	1	0	0	0
Hakea	eriantha	Australia	1	1		5	Tree	14.04	NA	4	0	1	Wind	NA	NA	1229228	NA	0	0	1	0	0	0
Hakea	epiglottis	Australia	1			3	Shrub	4.52	NA	5	NA	1	Wind	NA	0	79531	NA	0	0	0	1	0	0
Hakea	francisiana	Australia	1	1		8	Tree	9.7	NA	4	1	1	Wind	1	NA	1831478	NA	0	0	0	1	0	0
Hakea	gibbosa	Australia	1		1	3	Shrub	43.9	1	4	1	1	Wind	0	NA	165265	NA	0	0	1	0	0	0
Hakea	laurina	Australia	1	1		6	Tree	21.6	NA	5	1	1	Wind	1	NA	589484	Sus	0	1	1	0	0	0
Hakea	leucoptera	Australia	1			8	Tree	22.27	NA	3	0	1	Wind	1	NA	2808108	NA	0	0	1	0	0	0
Hakea	lissocarpha	Australia	1	1		3	Shrub	23.9	NA	5	1	1	Wind	0	NA	382213	Res	0	0	1	0	0	0
Hakea	lissosperma	Australia	1			5	Shrub	20.14	NA	3	NA	1	Wind	NA	NA	102594	NA	0	0	1	0	0	0
Hakea	microcarpa	Australia	1			2	Shrub	4.43	NA	6	NA	0	Wind	NA	NA	1353637	NA	0	0	0	1	0	0
Hakea	minyma	Australia	1			6	Shrub	6.55	NA	4	1	1	Wind	0	NA	859817	NA	0	0	1	0	0	0
Hakea	multilineata	Australia	1			5	Shrub	12.2	NA	4	1	1	Wind	1	NA	273137	NA	0	1	0	1	0	0
Hakea	nodosa	Australia	1			4	Shrub	13.98	NA	4	NA	1	Wind	NA	NA	169598	Sus	0	0	0	1	0	0
Hakea	orthorrhyncha	Australia	1	1		1.3	Shrub	25.7	NA	5	0	1	Wind	1	NA	26261	NA	0	0	0	1	0	0
Hakea	oleifolia	Australia	1			10	Tree	5	NA	3	NA	1	Wind	0	NA	69725	Sus	0	0	0	1	0	0
Hakea	pandanicarpa subsp. crassifolia	Australia	1			3	Shrub	75.8	NA	3	1	1	Wind	NA	NA	64813	Sus	0	0	1	1	0	0
Hakea	petiolaris	Australia	1			3.6	Shrub	17	NA	3	0	1	Wind	1	NA	81962	Res	0	1	1	1	0	0
Hakea	platysperma	Australia	1			2	Shrub	501.8	NA	4	1	1	Wind	1	NA	204927	NA	0	0	0	1	0	0
Hakea	prostrata	Australia	1	1		4	Shrub	60	NA	4	0	1	Wind	0	NA	412931	Sus	0	0	1	0	0	0
Hakea	purpurea	Australia	1			2.5	Shrub	NA	NA	3	1	1	Wind	NA	NA	444646	NA	0	0	0	0	0	0
Hakea	pycnoneura	Australia	1	1		2.5	Shrub	5.8	NA	4	1	1	Wind	1	NA	217802	NA	0	0	0	0	0	0
Hakea	salicifolia	Australia	1		1	8	Shrub	20.2	1	4	1	1	Wind	0	1	775663	NA	0	0	1	0	0	0
Hakea	scoparia	Australia	1			3.5	Shrub	3.79	NA	5	1	1	Wind	1	NA	272828	NA	0	0	0	1	0	0
Hakea	sericea	Australia	1		1	4	Shrub	31.7	1	4	1	1	Wind	0	NA	269565	NA	0	0	1	0	0	0
Hakea	teretifolia	Australia	1	1		2.6	Shrub	9.48	NA	6	0	NA	Wind	1	NA	543909	NA	0	0	0	1	0	0
Hakea	undulata	Australia	1	1		2	Shrub	16.6	NA	4	1	1	Wind	0	NA	127750	Sus	0	0	0	1	0	0
Hakea	ulicina	Australia	1			5	Shrub	6.42	NA	2	1	1	Wind	0	NA	129214	Sus	0	0	0	1	0	0
Hakea	victoriae	Australia	1			3	Shrub	21.2	NA	4	1	1	Wind	1	NA	16566	Sus	0	0	0	1	0	0
Grevillea	acanthifolia	Australia	1			1.5	Shrub	NA	NA	9	1	0	Ants	1	NA	70308	NA	1	0	1	1	1	0
Grevillea	alpina	Australia	1			2	Shrub	NA	NA	6	1	0	Birds	NA	NA	651522	VS	0	0	0	1	1	0
Grevillea	aquifolium	Australia	1	1		2	Shrub	NA	NA	4	0	0	Birds	NA	NA	142142	VS	0	0	0	1	0	0
Grevillea	arenaria	Australia	1	1		4	Shrub	NA	NA	12	1	0	Ants	1	NA	211119	NA	0	0	1	1	0	0
Grevillea	arenaria subsp. canescens	Australia	1			3	Shrub	NA	NA	12	0	0	Ants	1	NA	110897	NA	0	1	1	1	0	0
Grevillea	aspleniifolia	Australia	1	1		5	Shrub	86.96	NA	5	1	0	Wind	1	NA	8756	NA	1	1	1	0	1	0
Grevillea	australis	Australia	1			3	Shrub	14.115	NA	5	1	0	Insects	NA	NA	72054	NA	0	0	1	1	0	0

Grevillea	baileyana	Australia	1			30	Tree	14	NA	5	1	0	NA	1	NA	70737	NA	1	1	0	1	1	0
Grevillea	banksii	Australia	1		1	10	Tree	19.18	1	3	1	0	Wind	1	1	352611	NA	1	0	1	1	1	1
Grevillea	banyabba	Australia	1			1.5	Shrub	NA	NA	3	1	0	NA	NA	NA	329	NA	0	0	0	1	0	0
Grevillea	barklyana	Australia	1			8	Tree	136	2	3	1	0	Birds	NA	NA	485	NA	1	0	0	1	1	0
Grevillea	baueri	Australia	1	1		1	Shrub	NA	NA	5	1	0	Unspec	1	NA	221007	NA	0	0	0	1	0	0
Grevillea	beadleana	Australia	1			2.5	Shrub	NA	NA	3	1	0	NA	1	1	11426	NA	0	1	0	1	0	0
Grevillea	bedggoodiana	Australia	1			0.5	Shrub	NA	NA	2	1	0	Ants	NA	NA	135	NA	0	0	0	0	0	0
Grevillea	bipinnatifida	Australia	1			1	Shrub	NA	NA	7	0	0	Birds	NA	NA	46717	NA	1	0	0	1	0	0
Grevillea	biternata	Australia	1	1		2.5	Shrub	NA	NA	5	1	0	Insects	NA	NA	224113	NA	0	0	1	1	1	0
Grevillea	caleyi	Australia	1			4	Shrub	298.3	4	5	1	0	Unspec	1	1	9457	NA	0	0	0	1	0	0
Grevillea	confertifolia	Australia	1			1	Shrub	NA	NA	5	1	0	NA	NA	NA	35099	Sus	0	0	0	1	0	0
Grevillea	crithmifolia	Australia	1			2.5	Shrub	NA	NA	7	0	0	NA	NA	NA	42527	NA	0	0	0	1	0	0
Grevillea	curviloba	Australia	1			2.5	Shrub	NA	NA	3	1	0	NA	NA	NA	378	Sus	0	0	0	1	0	0
Grevillea	dryandri	Australia	1			2	Shrub	NA	NA	7	0	0	NA	NA	NA	431754	NA	1	0	0	1	1	0
Grevillea	evansiana	Australia	1			0.5	Shrub	NA	NA	5	1	0	Wind	NA	NA	7270	NA	0	0	0	1	0	0
Grevillea	endlicheriana	Australia	1			3	Shrub	NA	NA	5	NA	0	NA	NA	NA	13050	NA	0	0	0	1	0	0
Grevillea	fasciculata	Australia	1			1.8	Shrub	NA	NA	7	1	0	NA	NA	NA	39748	Sus	0	0	0	1	1	0
Grevillea	floribunda	Australia	1	1		2	Shrub	24.37	NA	7	0	0	Ants	1	NA	863097	NA	0	0	0	1	0	0
Grevillea	fulgens	Australia	1			3	Shrub	NA	NA	5	1	0	NA	NA	NA	2163	Sus	0	0	0	1	0	0
Grevillea	glauca	Australia	1			10	Shrub	72.77	NA	5	0	0	NA	1	NA	616894	NA	0	0	0	0	1	0
Grevillea	hilliana	Australia	1	1		30	Tree	NA	NA	6	1	0	NA	1	NA	325447	NA	1	0	0	1	1	0
Grevillea	iaspicula	Australia	1			1.5	Shrub	NA	NA	7	1	0	NA	1	0	253	NA	0	0	0	1	0	0
Grevillea	intricata	Australia	1			3	Shrub	NA	NA	6	1	0	NA	1	NA	17279	NA	0	0	0	1	0	0
Grevillea	involucrata	Australia	1			0.5	Shrub	NA	NA	5	1	0	NA	NA	NA	3735	Sus	0	0	0	1	0	0
Grevillea	johnsonii	Australia	1			4.5	Shrub	NA	NA	4	0	0	Ants	1	NA	25785	NA	0	0	1	1	0	0
Grevillea	juniperina	Australia	1	1		1.5	Shrub	NA	NA	4	1	0	Ants	1	NA	211941	NA	0	0	0	1	1	0
Grevillea	juniperina subsp. amphitricha	Australia	1			1.2	Shrub	NA	NA	2	1	0	Ants	1	NA	8987	NA	0	0	0	1	0	0
Grevillea	juniperina subsp. sulphurea	Australia	1			2	Shrub	NA	NA	2	1	0	Ants	1	NA	3192	NA	0	0	0	1	0	0
Grevillea	lanigera	Australia	1			2	Shrub	NA	NA	6	1	0	Ants	1	NA	240403	NA	0	0	0	0	1	0
Grevillea	laurifolia	Australia	1	1		0.1	Shrub	NA	NA	5	1	0	Ants	NA	NA	6967	NA	0	0	0	1	0	0
Grevillea	lavandulacea	Australia	1	1		1.5	Shrub	NA	NA	6	1	0	NA	1	1	326535	VS	0	0	1	1	1	0
Grevillea	leucopteris	Australia	1	1		5	Shrub	NA	NA	7	1	0	Wind	1	1	47833	NA	0	0	0	1	1	0
Grevillea	levis	Australia	1			2	Shrub	14.74	NA	6	0	0	NA	1	NA	197907	NA	0	0	0	1	0	0
Grevillea	linearifolia	Australia	1			2	Shrub	24	5	5	1	0	Ants	0	1	318931	NA	0	0	0	1	1	0
Grevillea	longifolia	Australia	1	1		6	Shrub	127.5	NA	7	1	0	NA	NA	1	5935	NA	0	0	0	1	0	0
Grevillea	longistyla	Australia	1			5	Shrub	NA	NA	4	0	0	NA	1	NA	401692	NA	1	1	0	1	0	0
Grevillea	manglesii	Australia	1			2.5	Shrub	NA	NA	6	1	0	NA	NA	NA	63190	NA	0	0	0	1	1	0
Grevillea	manglesii subsp. ornithopoda	Australia	1			2	Shrub	NA	NA	7	1	0	NA	NA	NA	2535	NA	0	0	0	1	1	0

Grevillea	mucronulata	Australia	1			3.5	Shrub	NA	NA	6	1	0	Ants	1	1	52217	NA	0	0	0	0	0	0
Grevillea	monticola	Australia	1			2	Shrub	NA	NA	5	1	0	NA	NA	NA	12417	NA	0	0	1	1	0	0
Grevillea	nudiflora	Australia	1			0.3	Shrub	NA	NA	5	0	0	NA	1	NA	382067	NA	0	0	0	1	0	0
Grevillea	obtusiflora	Australia	1	1		0.7	Shrub	NA	NA	4	0	0	NA	1	0	38472	NA	0	0	0	1	0	0
Grevillea	olivacea	Australia	1			4	Shrub	NA	NA	5	1	0	NA	1	NA	10850	Sus	0	0	1	1	0	0
Grevillea	oxyantha	Australia	1	1		3	Shrub	NA	NA	5	1	0	NA	NA	NA	19137	NA	0	0	0	1	0	0
Grevillea	paniculata	Australia	1			3	Shrub	14.62	NA	6	0	0	NA	1	NA	226066	NA	0	0	1	1	0	0
Grevillea	papuana	New Guinea	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	107934	NA	NA	0	0	0	0	0
Grevillea	parvula	Australia	1			2	Shrub	NA	NA	6	1	0	NA	1	NA	104194	NA	0	0	0	1	0	0
Grevillea	pimeleoides	Australia	1			2.5	Shrub	NA	NA	5	1	0	NA	NA	NA	2060	Sus	0	0	0	1	0	0
Grevillea	pteridifolia	Australia	1			15	Tree	17.71	NA	8	0	0	Ants	1	NA	3516070	NA	1	1	0	0	1	0
Grevillea	pterosperma	Australia	1			4	Shrub	29.16	NA	8	1	0	NA	NA	NA	3163957	NA	0	0	0	1	0	0
Grevillea	pulchella	Australia	1			1.5	Shrub	NA	NA	4	1	0	NA	NA	NA	226506	NA	0	0	0	1	1	0
Grevillea	quercifolia	Australia	1			0.7	Shrub	NA	NA	3	0	0	NA	1	NA	63995	NA	0	0	0	1	0	0
Grevillea	repens	Australia	1			NA	Shrub	NA	NA	7	1	0	NA	1	0	11812	NA	0	0	0	1	0	0
Grevillea	rhyolitica	Australia	1			2	Shrub	NA	NA	4	1	0	NA	1	NA	872	NA	0	0	0	1	0	0
Grevillea	robusta	Australia	1		1	40	Tree	20	6	5	1	0	Wind	1	1	1153696	NA	1	0	1	1	1	1
Grevillea	rosmarinifolia	Australia	1	1		2	Shrub	18.69	NA	6	0	0	Ants	1	NA	404678	NA	0	0	1	1	1	0
Grevillea	rosmarinifolia subsp. glabella	Australia	1	1		2	Shrub	NA	NA	4	1	0	Ants	1	NA	225976	NA	0	0	0	1	0	0
Grevillea	sericea	Australia	1			2	Shrub	15.901	5	7	1	0	Ants	0	1	118440	NA	0	0	0	1	1	0
Grevillea	shiressii	Australia	1			5	Shrub	25	NA	6	1	0	Ants	1	NA	5888	NA	0	0	0	1	0	0
Grevillea	speciosa	Australia	1			3	Shrub	27	2	4	1	0	Ants	1	NA	45163	NA	0	0	0	1	1	0
Grevillea	thelemanniana	Australia	1			1	Shrub	NA	NA	4	0	0	NA	1	NA	49559	Sus	0	0	0	1	1	0
Grevillea	thyrsoides	Australia	1			0.3	Shrub	NA	NA	4	1	0	NA	1	NA	474684	NA	0	0	0	1	0	0
Grevillea	tridentifera	Australia	1			NA	Shrub	NA	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	0	0	1	0	0
Grevillea	trifida	Australia	1	1		1.7	Shrub	NA	NA	5	1	0	NA	NA	NA	82752	NA	0	0	1	1	0	0
Grevillea	tripartita	Australia	1			3	Shrub	NA	NA	4	1	0	NA	NA	NA	61035	Sus	0	0	0	1	1	0
Grevillea	venusta	Australia	1			5	Shrub	NA	NA	4	1	0	NA	1	NA	3243	NA	0	0	0	1	0	0
Grevillea	vestita	Australia	1			4.5	Shrub	NA	NA	5	0	0	NA	NA	NA	125200	NA	0	0	1	1	0	0
Grevillea	victoriae	Australia	1			3	Shrub	NA	NA	4	1	0	NA	1	NA	392424	NA	0	0	0	1	0	0
Grevillea	wilsonii	Australia	1			1.5	Shrub	56.18	NA	6	0	0	NA	1	1	33274	Res	0	0	1	0	1	0
Finschia	chloroxantha	New Guinea	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	721453	NA	NA	0	0	0	0	0
Macadamia	hildebrandii	Indonesia	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	0	0
Macadamia	integrifolia	Australia	1	1		18	Tree	NA	NA	3	1	0	Mammals	0	NA	42858	NA	1	1	0	0	0	0
Macadamia	ternifolia	Australia	1	1		10	Tree	NA	NA	2	1	0	Mammals	0	NA	140655	NA	1	1	0	0	0	0
Macadamia	tetraphylla	Australia	1	1		18	Tree	NA	6	3	1	0	Mammals	0	1	453799	NA	1	1	0	1	0	0
Panopsis	cinnamomea	America	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1346	NA	NA	0	0	0	0	0
Panopsis	suaveolens	America	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1727569	NA	NA	0	0	0	0	0
Virotia	leptophylla	New Cal	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	0	0
Sleumerodendron	austrocaledonicum	New Cal	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	671	NA	NA	0	0	0	0	0

Bleasdalea	bleasdalei	Australia	1			24	Tree	NA	NA	4	NA	0	NA	NA	NA	39637	NA	1	0	0	0	0	0
Kermadecia	rotundifolia	New Cal	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	0	0
Kermadecia	sinuata	New Cal	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	111	NA	NA	0	0	0	0	0
Turrillia	lutea	Pacific islands	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	0	0
Turrillia	ferruginea	Pacific islands	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	0	0
Petrophile	pulchella	Australia	1			3	Shrub	4.96	4	8	1	1	Unspec	0	NA	120384	NA	0	0	0	1	0	0
Conospermum	triplinervium	Australia	1			4	Tree	NA	NA	3	1	0	NA	0	NA	452446	VS	NA	1	0	0	0	0
Buckinghamia	celsissima	Australia	1			30	Tree	NA	NA	4	1	0	Wind	0	NA	103344	NA	1	0	1	1	1	0
Lambertia	formosa	Australia	1			2	Shrub	20.9	3	5	0	1	Wind	1	NA	251052	VS	0	0	0	1	0	0
Lambertia	inermis	Australia	1			6	Shrub	NA	NA	10	1	1	Wind	1	NA	110786	VS	0	0	0	1	0	0
Alloxylon	pinnatum	Australia	1			25	Tree	NA	NA	3	1	0	Wind	1	NA	49461	NA	1	0	0	1	0	0
Alloxylon	flammeum	Australia	1			33	Tree	NA	NA	3	1	0	Wind	1	NA	5522	NA	0	0	0	1	0	0
Alloxylon	wickhamii	Australia	1			30	Tree	NA	NA	2	1	0	Wind	NA	NA	7891	NA	1	0	0	1	0	0
Brabejum	stellatifolium	Sthn Afr	1			8	Tree	NA	NA	2	0	0	Water	0	NA	45691	Sus	0	0	1	1	0	0
Garnieria	spathulifolia	New Cal	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	0	0
Lomatia	dentata	America	1			10	Tree	NA	NA	NA	NA	0	NA	NA	NA	114665	NA	NA	0	0	0	0	0
Lomatia	ferruginea	America	1			10	Tree	NA	NA	3	NA	0	NA	NA	NA	255980	NA	0	0	0	1	0	0
Lomatia	fraseri	Australia	1			11	Tree	7.2	NA	3	1	0	Wind	0	NA	436709	NA	1	0	0	1	0	0
Lomatia	fraxinifolia	Australia	1			24	Tree	25	NA	3	1	0	Wind	0	NA	15912	Sus	1	0	0	1	0	0
Lomatia	hirsuta	America	1			15	Tree	6.95	NA	4	NA	0	NA	NA	NA	NA	NA	NA	0	0	1	1	0
Lomatia	ilicifolia	Australia	1			3	Shrub	NA	NA	4	0	0	Wind	NA	NA	240164	Sus	1	0	0	1	0	0
Lomatia	myricoides	Australia	1			6	Shrub	6.45	NA	3	1	0	Wind	NA	NA	402214	NA	1	1	1	0	0	0
Lomatia	polymorpha	Australia	1			4	Shrub	NA	NA	3	NA	0	Wind	NA	NA	40059	NA	NA	0	0	1	0	0
Lomatia	silaifolia	Australia	1			2	Shrub	NA	NA	6	0	0	Wind	0	1	1366273	NA	1	1	0	1	0	0
Lomatia	tinctoria	Australia	1			2	Shrub	NA	NA	4	0	0	Wind	NA	NA	80246	NA	0	0	0	1	0	0
Mimetes	argenteus	Sthn Afr	1			3.5	Shrub	28.57	6	4	1	0	Ants	1	NA	1092	NA	1	0	0	1	0	0
Mimetes	cucullatus	Sthn Afr	1			2	Shrub	37.03	1	12	0	0	Ants	1	NA	67281	NA	1	1	0	1	0	0
Mimetes	hirtus	Sthn Afr	1			2.5	Shrub	13.49	3	7	1	0	Ants	1	NA	1668	Sus	1	0	0	1	0	0
Mimetes	hottentoticus	Sthn Afr	1			3	Shrub	NA	8	5	1	0	Ants	1	NA	10	NA	1	0	0	1	0	0
Oreocallis	grandiflora	America	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	0	0
Spatalla	setacea	Sthn Afr	1			1	Shrub	NA	4	3	1	0	Ants	0	NA	826	NA	0	0	0	1	0	0
Toronia	toru	New Zealand	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	46	NA	NA	0	0	0	0	0
Virotia	neurophylla	New Cal	1			NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	0	0	0	0
Stirlingia	latifolia	Australia	1			1.5	Shrub	NA	2	2	0	NA	NA	0	NA	154730	Sus	1	1	0	1	0	0
Symphionema	paludosum	Australia	1			0.6	Shrub	NA	NA	4	NA	NA	NA	NA	NA	148823	NA	0	0	0	0	0	0
Xylomelum	occidentale	Australia	1			8	Tree	NA	NA	3	0	1	NA	0	NA	33724	Sus	1	1	0	1	0	0
Hollandaea	riparia	Australia	1			NA	Tree	NA	NA	NA	NA	NA	NA	NA	NA	131	NA	1	0	0	0	0	0
Athertonia	diversifolia	Australia	1			30	Tree	NA	NA	4	NA	0	Mammals	NA	NA	5253	NA	1	1	0	1	0	0
Hicksbeachia	pinnatifolia	Australia	1			10	Tree	NA	NA	3	0	0	NA	NA	1	164360	NA	1	1	0	1	0	0
Persoonia	pinifolia	Australia	1			4	Shrub	141.518	NA	4	1	0	Birds	0	NA	12424	NA	1	0	0	1	0	0

Table S5. Significance of native range size (km^2) in the linear regression model fitted to species regions of origin. Home range size differed significantly between Australia and other regions of origin.

Coefficients	**Estimate**	**Standard error**	***t* - value**	***p*- value**
Intercept	8.384	0.172	48.7	< 0.05
Region of origin	2.771	0.233	11.87	< 0.05

Table S6. Vectors of dispersal for introduced, naturalized and invasive Australian species. Limited dispersal mode describes species with no obvious dispersal mechanism and species dispersed by gravity.

Status	**Ants**	**Birds**	**Insects**	**Limited**	**Mammals**	**Wind**
Introduced (not yet naturalized)	16	4	1	8	1	71
Naturalized (not yet invasive)	6	1	1	1	3	33
Invasive	0	0	0	0	0	8

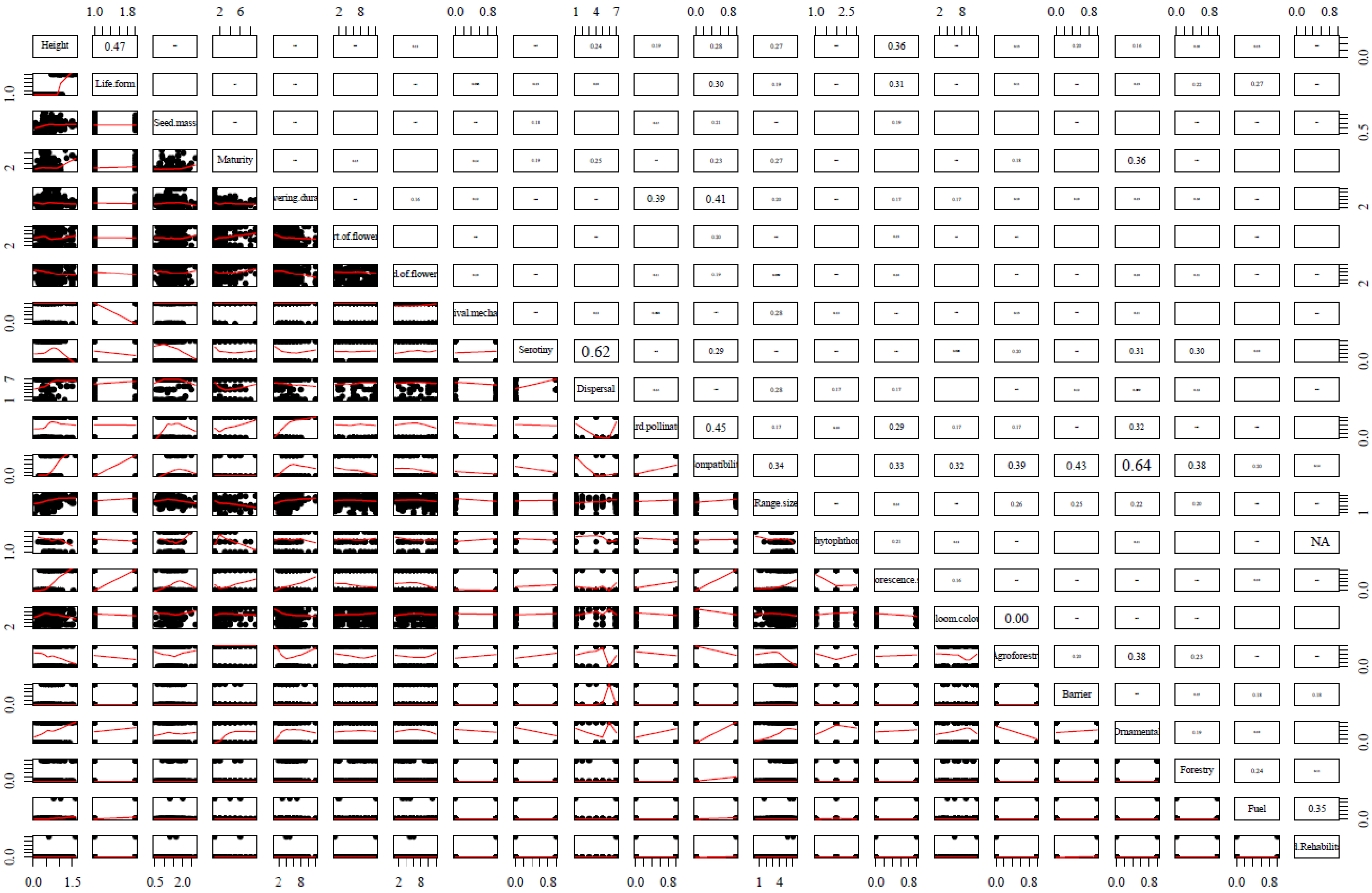
Supplementary Figure Legends

Figure S1. Correlation (*r*) tests between all predictor variables using the global dataset.

Figure S2. Plots of fitted functions for each term in the BRT naturalization model. This model only includes species native to Australia. Fitted functions depict the effect of each predictor variable after accounting for the effects of the other predictors in the model. Plots are ordered by the contribution of each variable, in parentheses.

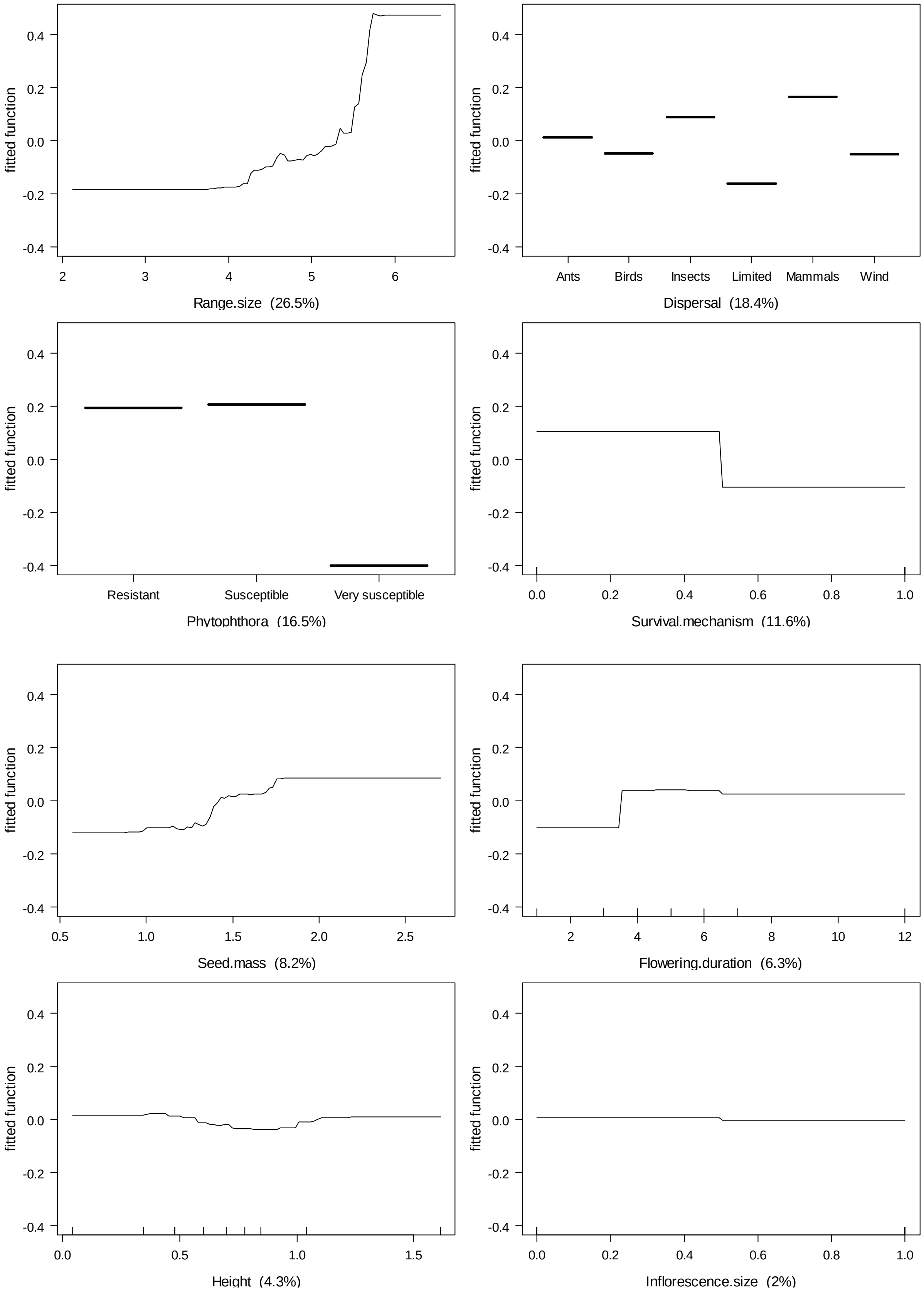
Figure S3. Plots of fitted functions for each term in the BRT invasion model. This model only includes species native to Australia. Plots are ordered by the contribution of each variable, in parentheses.

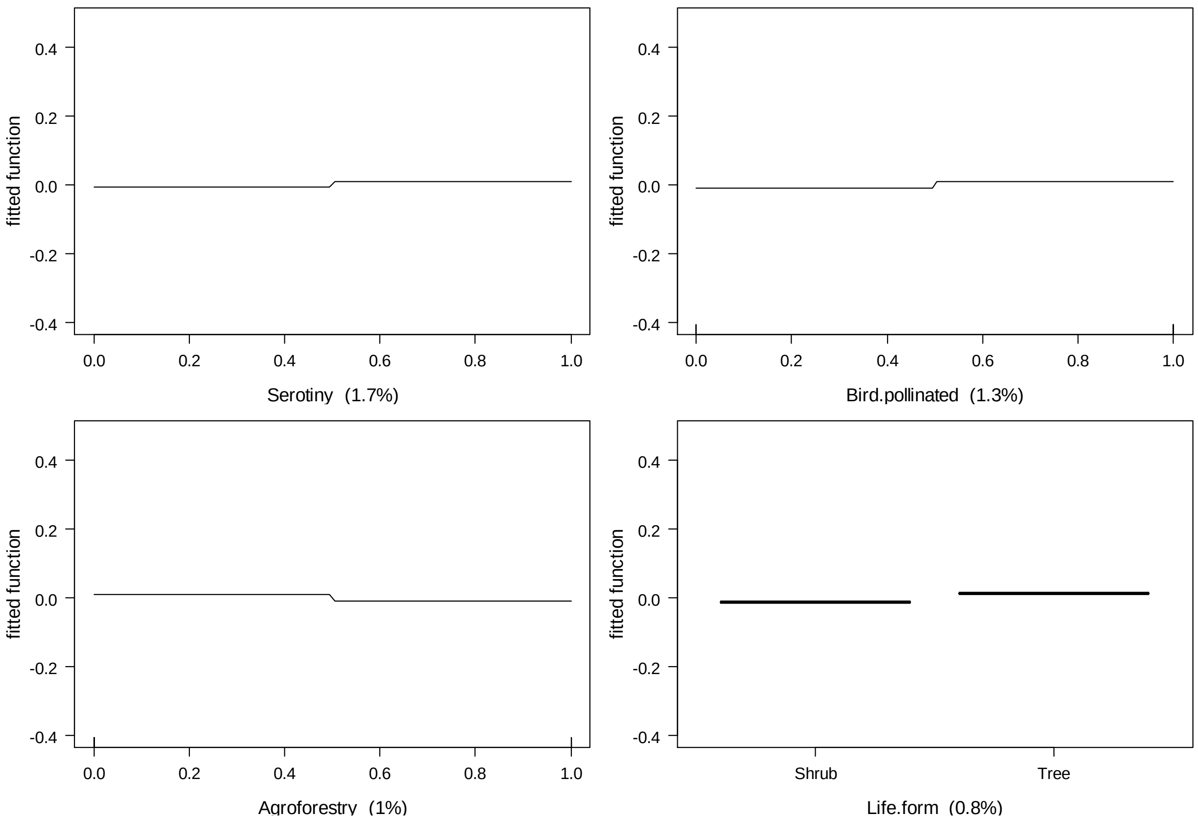
Figure S1

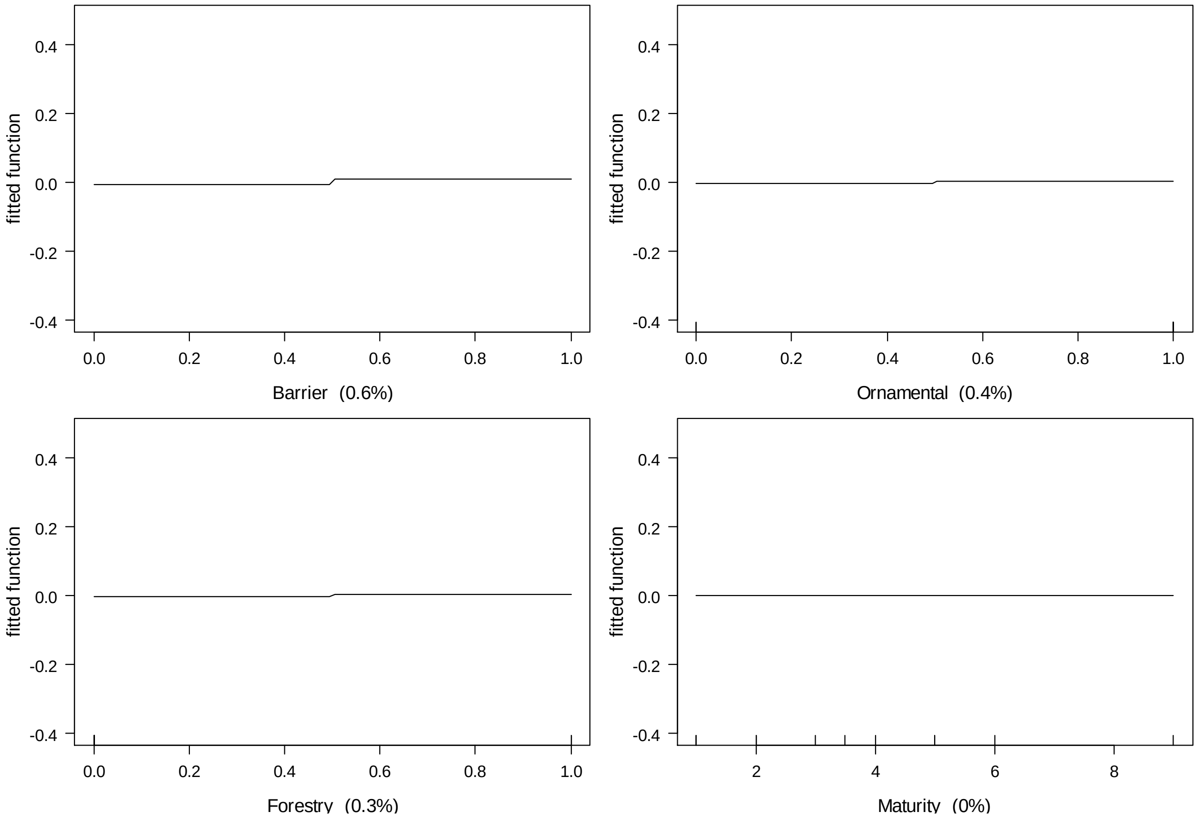


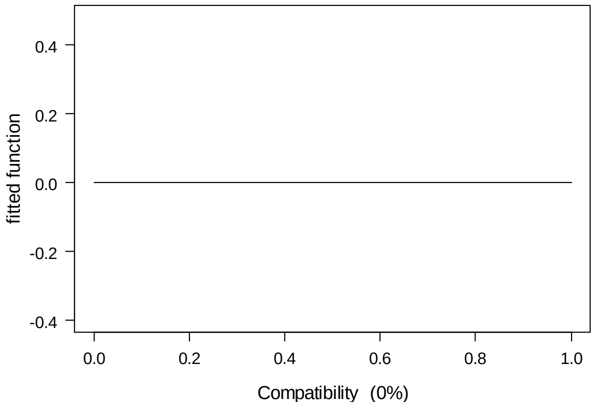
Height
Life.form
Seed.mass
Maturity
vering.dura
rt.of.flower
d.of.flower
ival.mecha
Serotiny
Dispersal
rd.pollinat
ompatibilit
Range.size
hytophthor
orescence.
loom.colo
Agroforestr
Barrier
Ornamental
Forestry
Fuel
l.Rehabilit
0.47
0.36
0.24
0.28
0.27
0.30
0.31
0.27
0.25
0.23
0.36
0.39
0.41
0.62
0.29
0.31
0.30
0.28
0.45
0.29
0.32
0.34
0.33
0.32
0.39
0.43
0.64
0.38
NA
0.00
0.38
0.35
1.0
1.8
2
6
8
0.0
0.8
1
4
7
2.5
1.5
0.5
2.0
0.5

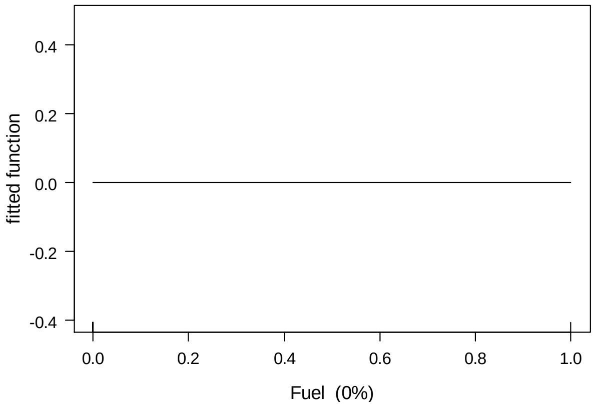
Figure S2


fitted function
0.4
0.2
0.0
-0.2
-0.4
2
3
4
5
6
Range.size (26.5%)
Ants
Birds
Insects
Limited
Mammals
Wind
Dispersal (18.4%)
Resistant
Susceptible
Very susceptible
Phytophthora (16.5%)
0.0
0.2
0.4
0.6
0.8
1.0
Survival.mechanism (11.6%)
0.5
1.0
1.5
2.0
2.5
Seed.mass (8.2%)
2
4
6
8
10
12
Flowering.duration (6.3%)
0.0
0.5
1.0
1.5
Height (4.3%)
0.0
0.2
0.4
0.6
0.8
1.0
Inflorescence.size (2%)


fitted function
0.4
0.2
0.0
-0.2
-0.4
0.0
0.2
0.4
0.6
0.8
1.0
Serotiny (1.7%)
Bird.pollinated (1.3%)
Agroforestry (1%)
Shrub
Tree
Life.form (0.8%)


fitted function
0.4
0.2
0.0
-0.2
-0.4
0.0
0.2
0.4
0.6
0.8
1.0
Barrier (0.6%)
Ornamental (0.4%)
Forestry (0.3%)
2
4
6
8
Maturity (0%)


fitted function
0.4
0.2
0.0
-0.2
-0.4
0.0
0.2
0.4
0.6
0.8
1.0
Compatibility (0%)


fitted function
0.4
0.2
0.0
-0.2
-0.4
0.0
0.2
0.4
0.6
0.8
1.0
Fuel (0%)

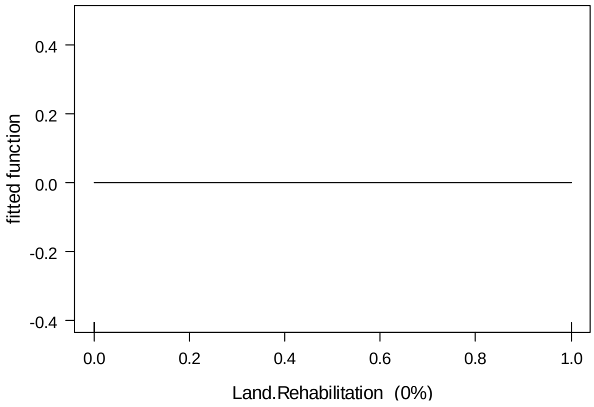
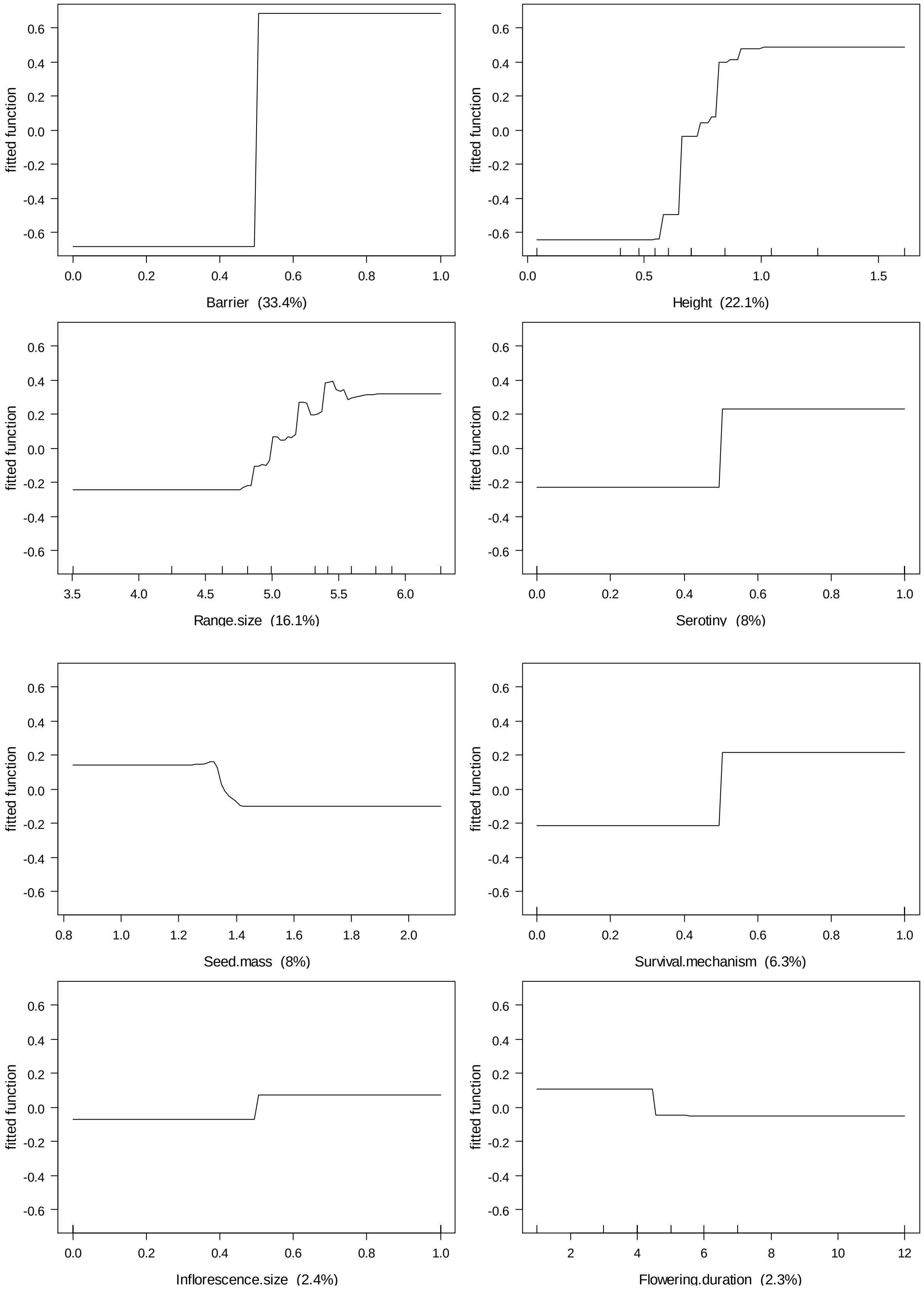
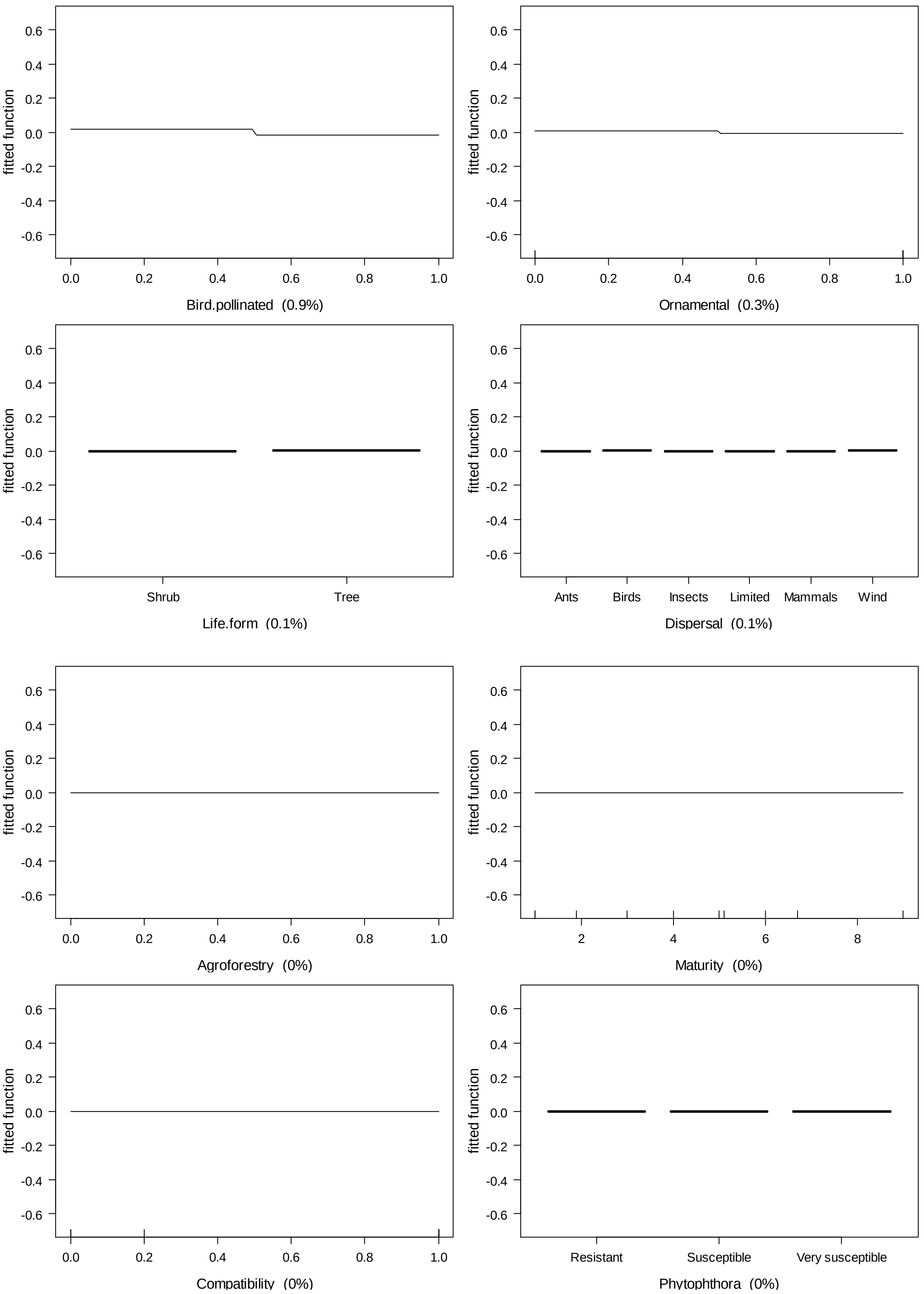
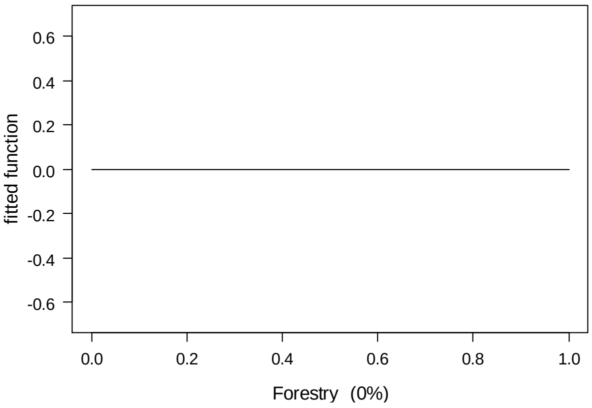
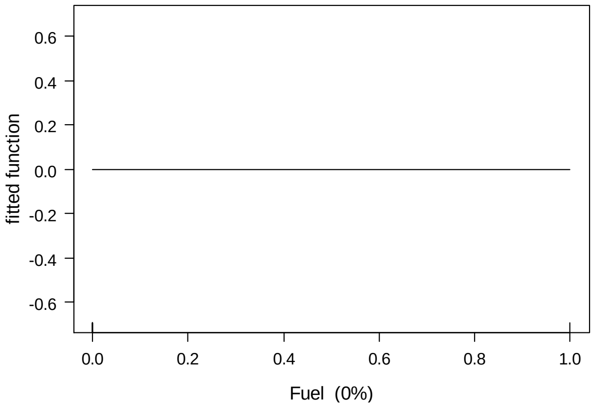

fitted function
0.4
0.2
0.0
-0.2
-0.4
0.0
0.2
0.4
0.6
0.8
1.0
Land.Rehabilitation (0%)

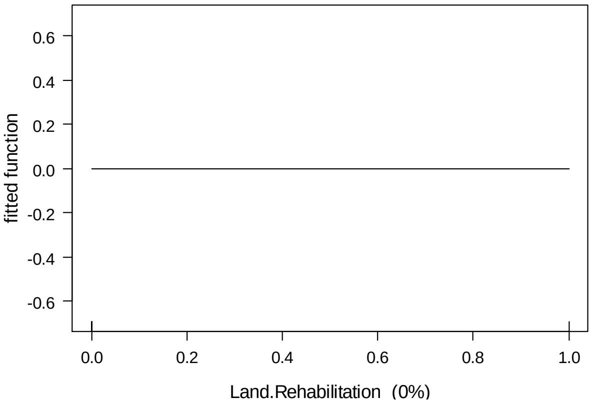
Figure S3


fitted function
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
0.0
0.2
0.4
0.6
0.8
1.0
Barrier (33.4%)
0.5
1.0
1.5
Height (22.1%)
3.5
4.0
4.5
5.0
5.5
6.0
Range.size (16.1%)
Serotiny (8%)
0.8
1.0
1.2
1.4
1.6
1.8
2.0
Seed.mass (8%)
Survival.mechanism (6.3%)
Inflorescence.size (2.4%)
2
4
6
8
10
12
Flowering.duration (2.3%)


fitted function
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
0.0
0.2
0.4
0.6
0.8
1.0
Bird.pollinated (0.9%)
Ornamental (0.3%)
Shrub
Tree
Life.form (0.1%)
Ants
Birds
Insects
Limited
Mammals
Wind
Dispersal (0.1%)
Agroforestry (0%)
2
4
6
8
Maturity (0%)
Compatibility (0%)
Resistant
Susceptible
Very susceptible
Phytophthora (0%)


fitted function
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
0.0
0.2
0.4
0.6
0.8
1.0
Forestry (0%)


fitted function
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
0.0
0.2
0.4
0.6
0.8
1.0
Fuel (0%)


fitted function
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
0.0
0.2
0.4
0.6
0.8
1.0
Land.Rehabilitation (0%)

Chapter 3: Determinants of naturalization and invasion: the case of alien Proteaceae in South Africa

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Contribution of each author:

DM, SG, DMR, JRUW: Planning of the study.

DM: Conducted all field work, statistical analyses and led the writing.

SG: Assisted with field work and writing.

TR: Provided information on field locations and commented on the manuscript

DMR: Provided comments on the manuscript and improved the writing.

JRUW: Provided comments on the manuscript and statistical advice.

Intended journal: *Austral Ecology*

Abstract

The outcome of plant introductions is often considered in binary terms (invasive or non-invasive). However, most species experience a time lag before naturalization occurs, and many species become naturalized at some sites but not at others. It is therefore important to understand the site-specific mechanisms underlying naturalization. We explore these issues by examining the status of introduced species of Proteaceae in South Africa that are not already classified as major invaders. At least 26 non-native Proteaceae species have been introduced to, and are cultivated in, South Africa. We mapped populations and examined differences between naturalized and non-naturalized populations (e.g. propagule pressure, land use and bioclimatic suitability). Of the 15 species surveyed, six species were naturalized at one or more sites. Of these, *Hakea salicifolia* is most widely cultivated, but is only naturalizing in some areas (32 naturalized populations out of 62 populations mapped). In suitable climatic conditions, propagule pressure was the most important determinant of naturalization for this species. In suboptimal climatic conditions, a combination of fine-scale determinants, including land disturbances and management activities facilitates naturalization. Similar explanations likely describe the variation in naturalization observed for other species - a long minimum residence time (*Banksia integrifolia*); influence of fires (*B. serrata*); absence of fires, substantial propagule pressure and poor land management (*B. formosa*), however there were few sites with which to compare against. As such we suggest that naturalization of Proteaceae in South Africa is strongly mediated by site-specific anthropogenic activities.

3.1 Introduction

Only a subset of introduced species become naturalized and only a subset of naturalized species become invasive (Williamson and Brown 1986). Climatic suitability (Richardson and Thuiller 2007), land use and human-mediated disturbance (Vilà and Ibáñez 2011), species traits (Pyšek and Richardson 2007), propagule pressure (Colautti *et al.* 2006; Lockwood *et al.* 2005), and residence time (Wilson *et al.* 2007) interact to mediate naturalization and invasion. Different factors assume particular importance at different spatial scales and at different stages of the introduction-naturalization-invasion (INI) continuum (Blackburn *et al.* 2011; Richardson and Pyšek 2012).

For a species to become invasive it must successfully progress through a number of barriers (Blackburn *et al.* 2011; Richardson *et al.* 2000). Most invasive alien plants were introduced intentionally through agriculture, forestry or horticultural pathways (Le Maitre *et al.* 2004; Reichard 2011; Richardson and Rejmánek 2011; Zalba and Villamil 2002). This allowed them to overcome the initial barrier of introduction. However, once introduced, survival, reproduction and dispersal barriers also need to be crossed for a species to successfully naturalize and become invasive.

Information is needed not only on species traits (i.e. invasiveness) but also on the susceptibility of the environment (i.e. invasibility), and how a species were brought to a new region (i.e. introduction dynamics). Many site factors can potentially facilitate invasions (Richardson and Pyšek 2006) but climatic suitability is generally considered as the most important prerequisite for naturalization and invasions (Guisan and Thuiller 2005; Mack 1996), although factors such a high propagule pressure can sometimes overcome barriers imposed by suboptimal environmental conditions (Rejmánek *et al.* 2005b).

The number of plants released into a novel environment, termed propagule pressure, is a fundamental predictor of invasion success (Colautti *et al.* 2006; Lockwood *et al.* 2005; Lonsdale 1999; Von Holle and Simberloff 2005). Species introduced in large numbers over a long period of time have a greater chance of establishing and spreading than those with lower propagule pressure (Dehnen-Schmutz and Touza 2008; Lockwood *et al.* 2005; Rouget and Richardson 2003; Simberloff 2009). Certain introduction pathways enhance the likelihood of invasive success by ensuring high propagule pressure (Wilson *et al.* 2009);

one such pathway is that associated with the introduction and dissemination of plants for horticulture (Dehnen-Schmutz *et al.* 2007; Lockwood *et al.* 2005).

Natural experiments involving the introduction of many species of different groups to many localities provide useful opportunities to draw important insights. For example work on several model groups in plant invasion ecology, such as *Pinus* and Australian *Acacia* species, provide general predictors for invasions (Rejmánek and Richardson 1996; Richardson *et al.* 2011). Other model groups are needed to provide additional insights for characteristics not well accommodated in these groups. Moreover, other groups can provide insight into whether the causes of invasions identified in these groups are more generally applicable.

Proteaceae is a large family of flowering plants with a long history of introduction to many parts of the world for horticulture (Sedgley *et al.* 2007). This family also includes species that were introduced recently (Sedgley *et al.* 2007), however introductions are on-going. Currently, of the 402 species which have been introduced globally only 14% have become naturalized and 2% are known to be invasive (D. Moodley, unpublished data). Given that many species have been introduced to many localities and these species occupy different stages in the invasion continuum, Proteaceae provides an excellent group to identify drivers of invasibility.

South Africa in particular has a substantial number of Australian Proteaceae (hereinafter referred to as proteas), which were introduced for use as barrier plants, ornamental purposes, food, cut-flowers and as landscape plants. At least 23 proteas have been introduced into South Africa (SAPIA, accessed November 2011; Rebelo 1991-2001; pers. obs.) and 11 species are recorded as naturalized (SAPIA; Figure 1). Three species (*Hakea drupacea* (C.F.Gaertn.) Roem. & Schult., *H. gibbosa* (Sm.) Cav., and *H. sericea* Schrad.) have become widespread invaders in South Africa, although in each case there are still climatically suitable areas of the country that are not yet invaded (Le Maitre *et al.* 2008; Richardson *et al.* 1987; Rouget *et al.* 2004). For other naturalized species we are beginning to understand the drivers of invasion, which include poor land management and particular fire regimes (Geerts *et al.* in review). In addition, many species are extensively cultivated (i.e. high introduction efforts) but have not yet become naturalized or a widespread invader. One such example is *Macadamia* F. Muell. species. South Africa is one of the world's largest producers of macadamia nuts and has for many years been home to large plantations of *Macadamia integrifolia* Maiden & Betche, *M. tetraphylla* L.A.S. Johnson and cultivars of these species (Mabiletsa 2004; Nagao 2011; The Southern African Macadamia Growers' Association, http://www.samac.org.za), but the species is not recorded in the Southern African Plant Invaders Atlas (accessed March 2012, http://www.agis.agric.za/wip/, ARC-Plant Protection Research Institute, Pretoria). Finally, some Proteaceae species are starting to become naturalized or invasive, but only at a few sites. Although evidence from around the world suggests that Proteaceae is not a particularly "weedy" family, at least 8 species of the 402 introduced species are invasive, this may be partly or largely due to the fairly recent history of introductions for many species. Growing interest in understanding the components of "invasion debt" will assist in the prediction and prevention of future invasions (Essl *et al.* 2011). We will gain a greater understanding of this issue by assessing the importance of site effects. Evidence is indeed emerging that some introduced Proteaceae species with a long history in South Africa are now showing signs of becoming naturalized. This even applies to *Hakea salicifolia* (Vent.) B.L.Burtt, a species widely planted as a hedge plant for at least a century and which has widely been considered a non-invasive option. These dynamics make proteas an ideal group to explore the site-specific factors determining invasions.

This study aimed to 1) determine the status of introduced Proteaceae species in South Africa; 2) conduct a qualitative assessment of factors explaining naturalization for Proteaceae in South Africa; and 3) analyse the factors affecting naturalization for *Hakea salicifolia* which has many naturalized and non-naturalized populations.

3.2 Methods

3.2.1 Study sites

We compiled a list of all recorded protea localities in Southern Africa, using the Protea Atlas Database and the Southern African Plant Invaders Atlas (SAPIA) as initial sources. Following detailed field searches we also added personal observations and information provided by farmers and land owners to the locality list. Our aim was to understand which site factors are important for triggering naturalization (i.e. transition from introduction to naturalization; Richardson and Pyšek 2012); we therefore excluded species that are already major invaders in southern Africa. This criterion was selected because we did not observe any sites where the widespread invaders have not yet naturalized. We did not consider *Grevillea robusta* A.Cunn. ex R.Br., a major invader in South Africa, because although widely planted it is only naturalized at a few sites and is therefore not classified as a widespread invader. Similarly, *B. ericifolia*, is only invasive at one site in South Africa and was not classified as a major invader. This resulted in a list of 411 alien protea localities in southern Africa (see Table 1 for species and localities mapped). For *H. salicifolia* and *G. robusta*, which are planted in many sites across South Africa, we selected sites across the distribution ranges of the species. We only conducted field surveys at sites where we thought populations may have a chance to spread (i.e. where plantings adjoin potentially invasible habitats; Figure 2).

3.2.2 Study species

3.2.2.1 Alien Proteaceae surveyed in South Africa and their invasion status globally

Of all introduced proteas in South Africa, the genus *Banksia* L.f. has the largest number of species. *Banksia ericifolia* and *B. integrifolia* are invasive and *B. serrata*, *B. spinulosa* and *B. formosa* (formerly *Dryandra formosa*) have naturalized elsewhere in the world. *Grevillea robusta* is recognized as a major invader globally (Table 1) but we included the species in our study as no populations were observed to be invading during initial surveys. In addition, *Macadamia integrifolia*, *M. tetraphylla* and *Telopea speciosissima* (Sm.) R.Br. are also naturalized in other parts of the world (Table 1).

3.2.2.2 *Hakea salicifolia*

Preliminary surveys found only one or two naturalized populations for all species except *H. salicifolia* (Table 1), and so *H. salicifolia* was selected for more detailed analysis. We selected sites across the range of this species. *H. salicifolia*, commonly referred to as Willow-leaf Hakea, comprises two subspecies with overlapping ranges: *H. salicifolia* subsp. *salicifolia* and *H. salicifolia* subsp. *angustifolia* (A.A.Ham.) W.R.Barker (Flora of Australia online at http://www.environment.gov.au/biodiversity/abrs/online-resources/flora/main/index.html). Although their ranges overlap, subsp. *angustifolia* is confined to the Sydney region of New South Wales and subsp. *salicifolia* is widespread along the coastal regions of Queensland and New South Wales (Figure 3a). These taxa differ in the width of their leaves; the leaves of subsp. *salicifolia* are more than seven millimetres whereas the width of subsp. *angustifolia* is between four and seven millimetres (New South Wales Flora online at http://plantnet.rbgsyd.nsw.gov.au). It is the latter subspecies that has been introduced to South Africa, since we only observed plants with leaves greater than seven millimetres in width, and will hereafter be referred to by its species name only.

Hakea salicifolia has been widely planted in South Africa across the fynbos, grassland and savanna biomes as a hedge plant and for windbreaks. It has naturalized and become invasive in several regions of the world (Table 1). It is an obligate seeder and is adapted to fire by possessing follicles that afford some protection for the seeds against fire (Protea Atlas Database). In New Zealand fires have successfully assisted the spread of *H. salicifolia* (Williams 1992). However, in South Africa spread of this species into fynbos vegetation may be limited because the follicle walls are too thin to protect seeds from typical fires in fynbos (Richardson *et al.* 1987). In this study, however, we found one population spreading after a fire, suggesting that seeds are able to survive some fires.

Of the naturalized Proteaceae in South Africa, *H. salicifolia* is intermediate in its adventive distribution. The species was for many years considered non-invasive. Indeed, its Afrikaans common name is “mak hakea” (meaning “tame hakea” in reference to its non-invasiveness relative to three other *Hakea* species). It was not listed among 84 “emerging invaders” in a national study that aimed to prioritize alien plant species and areas for management action (Nel *et al.* 2004). Although not listed under current legislation, it has been considered for listing.

3.2.3 Survey methods

At each site plants were measured and mapped using a hand-held GPS. Each site was systematically surveyed on foot at least 10 metres from any plants observed (in most cases plants could be seen much further than 10m away). Recruiting individuals were categorised as seedlings (<30cm); juveniles (>30cm, non-reproducing plants); and mature adults (>30cm, reproducing plants). At five sites with extensive recruitment, the number of plants was estimated by walking around the population to delimit the extent of the population;

placing transects through a part of the population that most accurately depicted the density and size classes; and counting all seedlings, juveniles and mature adults.

3.2.3.1 Designating invasion status

Following the scheme proposed by Richardson *et al*. (2000) and Pyšek *et al*. (2004), we classified populations as naturalized when self-sown mature plants were present (this also includes invasive populations where plants have spread more than one hundred metres within fifty years) and as non-naturalized populations when no self-sown mature plants was detected.

3.2.4 Which variables determines the invasion success of *Hakea salicifolia*

At each site we collected a variety of site-specific predictor variables (Table 2). These variables were selected based on the results of previous studies that assessed at how the recipient environment influences naturalization

Analyses were only conducted for *H. salicifolia* populations because of the small sample size of other surveyed species. First we screened pair-wise correlations between predictor variables to avoid including correlated variables in the model (Kendall rank correlation coefficient < 0.65). Accurate fire records were only available for two *H. salicifolia* populations and we do not know if other populations burned. Because this predictor was strongly correlated with other predictors we excluded this variable from the model (Figure S1). While the number of planted individuals in a population and seed output were inter-correlated (r~0.65), both were retained in the model.

The analyses were performed in two stages, first using all surveyed *H. salicifolia* populations (n=62). Preliminary tests revealed that bioclimatic variables, particularly precipitation, were important in explaining naturalization. This was only tested in the beginning for the first 37 sites, 14 non-naturalized and 23 naturalized populations, using data from the South African Weather Service. This prompted us to perform a bioclimatic model to assess climatic suitability for the species in South Africa. We found that a large proportion of populations occur in regions that are climatically suboptimal for this species which suggests that climate may serve as a barrier to naturalization. In an attempt to determine factors influencing naturalization, we only used sites in climatically suitable regions for the second part of the analysis.

3.2.4.1 Bioclimatic modelling

To determine the suitable climatic range of *H. salicifolia*, we developed a species distribution model using BIOMOD (Thuiller *et al.* 2009). As it does not have a wide invasive range in South Africa, we extracted geo-referenced distribution records from its native range (Atlas of Living Australia, www.ala.org.au, accessed May 2012). Records were scrutinized for synonyms, subspecies, missing coordinate data, spatial uncertainty, points in the ocean and duplicated locality points (n=181) which we omitted. BIOMOD requires presence absence data, we created 12000 pseudo absence points by sampling random points in the study area using the dismo package (Hijmans *et al.* 2012). The Köppen-Geiger vegetation mask was used to define the background points. This technique includes selecting random presence and absence points within biomes comprising species occurrences.

Environmental data on 30 arc-second resolution grids were downloaded from the WorldClim database (www.worldclim.org, accessed June 2012). We observed that populations located in drier habitats die easily if they are not watered regularly. Thus, precipitation during the dry months is necessary for *H. salicifolia* to survive (pers. comm. with landowners). Therefore, we selected precipitation of the driest quarter as an important primary predictor variable and subsequent variable selection was based on predictors with the lowest pair-wise correlations (Kendall rank correlation coefficient < 0.6). We then ran generalized linear models using the selected variables and the final model was selected using the Akaike information criterion (AIC). This approach resulted in one rainfall (precipitation of the driest quarter) and two temperature (maximum temperature of the hottest month and mean temperature of the driest quarter) variables.

Our modelling technique included generalized boosted models with an optimum number of 2000 trees (GBM, Ridgeway 1999) which was incorporated in the BIOMOD package (Thuiller *et al.* 2009). The model was calibrated using 70% of the data and evaluated on the remaining 30%. In addition, the data splitting procedure was replicated four times using k-fold cross validation. The predictive power of the model was examined using the TSS (Allouche *et al.* 2006) and AUC (Hanley and McNeil 1982). The different models calibrated in Australia were then projected onto South Africa to identify areas with potentially suitable environmental conditions.

From the bioclimatic model output, we used a threshold of 25% which is representative of where *H. salicifolia* is likely to thrive because of suitable climatic conditions (n=26). This threshold was obtained from the models evaluation procedure using the true skill statistic (TSS, Allouche *et al.* 2006) and area under curve receiving operating characteristic curve (ROC, Hanley and McNeil 1982). These statistics give the cut off values for the model and represents the best probability of occurrence from the models prediction of presence-absence points (Thuiller *et al.* 2009).

The data were analyzed using generalized linear models (GLM) with binomial errors to test the significance of factors influencing the likelihood of populations naturalizing. The response variable was coded as 1 for naturalized populations and 0 for non-naturalized populations. All analyses were performed in R version 2.15.1 (R Development Core Team 2009). Because only a few variables were found to be significant, we only fitted single-predictor models and could not test for a minimum adequate model.

3.3. Results

Fifteen species of proteas comprising 145 populations were surveyed across South Africa (Table 1). All species, except *Grevillea robusta* and *H. salicifolia*, were recorded only from the Western Cape. During our surveys we found two species, *B. formosa* and *B. serrata*, that were not recorded in our database and were spreading. Several new *B. integrifolia* populations were also discovered, and one population in Pringle Bay is successfully invading (sensu Pyšek *et al.* 2004).

We recorded 117 *H. salicifolia* populations with a wide planted distribution throughout South Africa from Nieuwoudtville in the Northern Cape to Thohoyandou in Limpopo (Figure 3b). In total 62 populations were surveyed, comprising 32 naturalized and 30 non-naturalized sites.

Using all surveyed *H. salicifolia* populations, the number of seeds in a population, which we used as a proxy for propagule pressure, differed significantly between naturalized and non-naturalized populations (Table 3a). Populations with larger canopy-stored seed banks were more likely to naturalize (z = 2.31, P = 0.02, 95% CI = 0.06 to 0.50, Figure 4).

In the climate-informed analysis, we found three predictors driving naturalization: elevation, soil pH and the number of seeds in a population (Table 3b). Populations planted at lower elevations (e.g. the southern Cape) had a greater probability of naturalizing (z = -3.11, P = 0.001). However, our observations could contain some spatial autocorrelation- most of the naturalized populations were in a lowland region of the southern Cape and elevation is highly correlated with climatic variables.

The level of soil pH was also found to be important for species to successfully naturalize (z = 2.58, P = 0.01). Australian proteas grow mostly in soils with low-nutrient content and low pH (Myerscough *et al.* 2001). However, the naturalized *H. salicifolia* populations occurred mainly on neutral soils and non-naturalized populations were mostly present in slightly acidic soils (pH=6). Given that we obtained data from a global soil database, this could again be a result of spatial autocorrelation.

The total number of seeds in a population was an important determinant of naturalization in areas where climatic conditions are suitable (z = 1.95, P = 0.05, 95% CI = 0.12 to 1.12, Figure 5). We found no significant effect of propagule pressure in unsuitable sites (z = 1.41, P = 0.16, 95% CI = -0.07 to 0.52; Figure 4; Table S3), however this effect was also not significantly different from climatically suitable sites (z = 0.98, P = 0.32, 95% CI = -0.21 to 0.97; Table S3).

Although land use type had no significant effect on *H. salicifolia's* ability to spread, there is evidence that this species has the ability to naturalize in all areas where it is planted, particularly in disturbed sites (Figure S2). This suggests that land-use types do not limit spread. Thirty-nine percent of populations occurred along roads and many of these populations are naturalized. A concern is the species ability to naturalize in natural vegetation, although this was only observed at one site out of seven sites bordering natural vegetation.

Overall, the calibrated models show excellent predictive power (mean AUC = 0.95 and mean TSS = 0.82; see Table S1 & S2 for further details). The greatest numbers of planted *H. salicifolia* populations occur in the Western Cape which has low climatic suitability (Figure 3b). In contrast, *H. salicifolia* is not widely planted in regions with suitable climatic conditions. Populations in the Highveld region are few and non-naturalized. The only region with high climatic suitability and a large number (n=14) of planted populations is the George-Knysna region in the southern Cape and a small area in the Eastern Cape, where 13 (93%) of populations are naturalized.

3.4 Discussion

Our results provided a clear example of the conditional nature of invasions, with different factors driving naturalization of different species and at different sites. In particular, species have to be given a chance and the right conditions for spread. For *H. salicifolia* we were able to go further and determine that suitable climatic conditions and high propagule pressure significantly influence naturalization, but that it can perform well in regions predicted to be unsuitable provided populations are well maintained (e.g. adequate water supply) and the occurrence of human-mediated disturbances.

There is mismatch between the observed distribution of *H. salicifolia* and that defined as climatically suitable. The southern parts of the Western Cape, areas in the Eastern Cape, KwaZulu-Natal and the Highveld have climates similar to the native range of the species in south-eastern Australia, but *H. salicifolia* have not been widely planted in these regions. Seed output, used as a proxy for propagule pressure, was a significant driver of naturalization at these climatically suitable sites. This suggests that if *H. salicifolia* is planted more widely in climatically suitable areas, populations would have the ability to successfully overcome naturalization barriers. Human-mediated propagule pressure is therefore a crucial determinant of plant invasions on a regional scale. In addition, the Knysna region which has suitable climatic conditions also has many naturalized populations, and should be targeted for control.

On the other hand, *Hakea salicifolia* is planted widely in climatically unsuitable regions. The suboptimal climates, perhaps together with the fact that the follicles of this species provide inadequate protection of the seeds in intense fires that are characteristic of fynbos (Richardson *et al.* 1987), probably explains why the species has not become a major invader. We hypothesize that there are other factors which are overridingly important in explaining naturalization success at these climatically unsuitable sites. These include disturbance associated with road works (Figure 6a); hedges under pine plantations (Figure

6b); steep slopes; seepage areas; high propagule pressure in a confined space (Figure 6c) and when plants are watered regularly (Figure 6d).

3.4.1 Qualitative analysis of site limitations for other alien protea species

Disturbance also appears to be important for successful naturalization of other alien proteas in South Africa. Disturbed habitats generate conditions suitable for invasions because this reduces the limiting effects of competition from resident vegetation (Pyšek *et al.* 2010; Richardson and Bond 1991). *Banksia formosa* and *B. serrata* show signs of becoming invasive in at least one population. These sites were not previously recorded. We observed that fire facilitated the spread of *B. serrata* and poor land management is driving spread in *B. formosa* populations.

The connection between fire and spread is likewise very strong (Geerts *et al.* in review). A stand of nine *B. serrata* trees were planted in natural fynbos in Betty's Bay approximately 14 years ago (pers. obs.). After fires in 1991 and 2010 (Cape Nature 2011), the population has expanded and is now well established with at least 10 seedlings, 34 juveniles and 11 self-reproducing mature trees. Only four *B. formosa* populations have been recorded, of which two are spreading. The two spreading populations are planted in large numbers for use as cut-flowers in a flower farm in Elim. Due to a lack of fire, substantial propagule pressure and poor management of these plantings, massive recruitment is occurring (at least 9000 mature plants were recorded in one population and 7 in the other).

Another important determinant of invasions is residence time (Pyšek *et al.* 2009; Wilson *et al.* 2007). Plants occupying an area for a longer period have a greater chance to spread more propagules and thus have a greater probability of becoming invasive (Rejmánek *et al.* 2005a). This characteristic provides a potential explanation for the spread of *Banksia integrifolia*. A single *B. integrifolia* tree was planted as an ornamental plant in Pringle Bay 33 years ago (pers. comm.). This is now an invasive population with several seedlings, juveniles and mature plants spread across a minimum distance of 253m in the natural vegetation. These cases demonstrate that fine-scale determinants are important triggers of naturalization in this group and that naturalization at regional scales occur when populations are given opportunities to spread (i.e. conditional invasions).

3.5 Conclusion

Our study confirms that on a regional scale naturalization of *H. salicifolia* is primarily determined by propagule pressure in areas where climatic conditions are suitable. However, several human-mediated factors potentially play a role in the successful naturalization of populations in areas with suboptimal climates. From this study we suspect that *H. salicifolia* will not become a major problem, particularly in the Western Cape where it is widely planted. However, if this species develops the inherent ability to expand its range in these suboptimal climates then species will thrive in this region. With the results from this study we recommend that *H. salicifolia* should not be planted widely in regions where climatic conditions are suitable, since then the risk of invasion is likely to be high. As such *H. salicifolia* could be regulated by area (category 2 invader on the draft regulations proposed under the National Environmental Management: Biodiversity Act (NEM:BA)), but in the southern Cape, *H. salicifolia* plantings should be prohibited, and eradication considered.

Disturbance regimes (i.e. natural and human-mediated) facilitate naturalization of several other alien proteas in South Africa (i.e. *B. formosa, B. integrifolia* and *B. serrata*). Furthermore, these observations suggest that fire regimes and residence time potentially describe characteristics which facilitate spread in this group. Since a few populations are already spreading, safety measures need to be established to prevent potential invasions of these species. Alternatively, eradication of these species is feasible because there are few populations, they are limited to the Western Cape, and species possess canopy stored seed banks (except *B. formosa*) that require fire for release.

Globally only 8 protea species are currently recognized as invaders, but in South Africa this study provides evidence that this number will potentially increase in the near future. These new invaders are mainly used for ornamental purposes, wind breaks and cut-flowers, we recommend that such activities be carefully monitored to prevent another wave of widespread invaders.

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Tables

Table 1. Description of non-invasive alien Proteaceae recorded in South Africa, the number of populations surveyed and population status.

Species	Number of sites recorded from databases	Number of surveyed sites in this study	Number of naturalized sites surveyed	Invasion status elsewhere
Banksia baxteri	2	0	NA	
Banksia coccinea	3	3	0	
Banksia ericifolia	15	15 (only 5 populations were found)	2	Naturalized in New Zealand [1]; Invasive in South Africa [2]
Banksia formosa	4	4	2	Naturalized in Australia [1,4]
Banksia hookeriana	3	1	0	
Banksia integrifolia	9	9	1	Naturalized in New Zealand [1], Azores [3] and Australia [4]; Invasive in Hawaii [5], beginning to invade in Kleinmond in the Western Cape, South Africa (this population has been cleared) [6]
Banksia prionotes	1	1	0	
Banksia serrata	1	1	1	Naturalized in New Zealand [1]
Banksia speciosa	7	4	0	
Banksia sphaerocarpa		0	NA	
Banksia spinulosa	2	2	0	Naturalized in Australia [1]
Grevillea banksii	18	0	NA	
Grevillea juniperina	1	0	NA	
Grevillea robusta	197	46	1	Invasive in South Africa [7,8], Hawaii, Brazil, Uganda and Guatemala [8], Reunion island [9], and many pacific islands [5]
Grevillea rosmarinifolia	1	0	NA	
Grevillea sericea	1	0	NA	
Hakea petiolaris	1	1	0	

Hakea salicifolia	133	62	32	Naturalized in New Zealand [1,10], South Australia, Victoria and Tasmania [1,4,11], France, Spain and Portugal [3,12], South Africa [1], Swaziland [13] and South India [14]; Invasive in Portugal, New Zealand and Australia [8]
Hakea victoriae	3	0	NA	
Macadamia integrifolia	3	2	0	Naturalized in Paraguay, New Zealand, Puerto Rico , United States [1] and Australia [4]
Macadamia tetraphylla	2	2	0	Naturalized in Paraguay, New Zealand, Hawaii [1] and in Australia [4]
Stenocarpus sinuatus	2	0	NA	
Telopea speciosissima	2	2	0	Australia [1]

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Table 2. Description of predictor variables and the methods used to obtain data for alien Proteaceae in South Africa.

Predictor variable	**Methods of measuring**	**Reference**
Elevation	GPS	
Age*****	Counted the number of whorls for *Banksia* species	Jenkins *et al*. (2005)
	Height was a measure of age for *Grevillea robusta* (cm). We used a crude estimate of a plant that we knew the age by counting age/growth rings.	T. Mullin (pers. com.)
	Measured stem diameter using callipers for *Hakea salicifolia* (cm)	Williams (1992)
Propagule pressure	Total number of planted individuals	
Propagule rain	Seed output was estimated by counting all the follicles on one planted individual and multiplying it by the number of seeds (2 winged seeds per follicle) and individuals. If the population comprised plants of different heights, we counted seed output for each height class.	
Height	Estimated height (cm)	
Time since last fire*****	Indicator species: age of re-seeding native Proteaceae	
Land use	Considered which land types are adjacent to the populations (in many cases there are more than one land use types)	
Management	Whether plants are cut or irrigated	
Biome	ArcMap was used to identify vegetation types	Mucina and Rutherford (2006)
Soil pH	Weighted average of pH values	Harmonized World Soil Database (2009)
Soil drainage	Drainage classes	Harmonized World Soil Database (2009)

***** Where possible we tried to get information from farmers or land owners.

Table 3. Linear regressions of the factors influencing naturalization of *Hakea salicifolia* populations in South Africa, using single predictor models. (a) All surveyed populations (n=62); (b) populations in areas with suitable climatic conditions (n=26). Mean and range of the data are given for continuous variables.

(a)

Variable	**Summary (median, range)**	**Test**	**Relationship**
Elevation	329, 42 - 1472	*z* = -1.785, *P* = 0.0743	No effect
Stem diameter	14, 4.10 - 30	*z* = 1.205, *P* = 0.228	No effect
Number of planted individuals (log transformed)	68, 1-1530	*z* = 0.632, *P* = 0.528	No effect
Seed output (log transformed)	144000, 0 - 13040000	*z* = 2.311, *P* = 0.0209	Populations with more seeds are more likely to naturalize
Height (log transformed)	544.5, 210 - 1075	*z* = -0.200, *P* = 0.842	No effect
Habitation		*z* = -0.699, *P* = 0.484	No effect
Natural vegetation		*z* = -0.430 , *P* = 0.667	No effect
Orchard		*z* = -0.128, *P* = 0.898	No effect
Pastoral land		*z* = -0.982, *P* = 0.326	No effect
Plantation		*z* = 1.610, *P* = 0.107	No effect
Rail/Road		*z* = 1.212, *P* = 0.226	No effect

Transformed		$z = 1.610$, $P = 0.107$	No effect
Vacant land		$z = -0.430$, $P = 0.667$	No effect
Management		$z = -0.922$, $P = 0.356$	No effect
Forest		$z = 0.007$, $P = 0.994$	No effect
Fynbos		$z = -0.007$, $P = 0.995$	No effect
Grassland		$z = -0.007$, $P = 0.994$	No effect
Savanna		$z = -0.011$, $P = 0.991$	No effect
Soil pH	7, 5 - 8	$z = 0.397$, $P = 0.691$	No effect
Soil drainage		$z = 1.760$, $P = 0.0784$	No effect

(b)

Variable	**Summary (median, range)**	**Test**	**Relationship**
Elevation	401.5, 155.0 -1472	*z* = -3.112, *P* = 0.00186	Populations at lower altitudes have a greater probability of naturalizing
Stem diameter	14, 4.10 - 30	*z* = 0.883, *P* = 0.377	No effect
Number of planted individuals (log transformed)	44, 0 - 402	*z* = -0.980, *P* = 0.327	No effect
Seed output (log transformed)	99117, 0 - 1557000	*z* = 1.954, *P* = 0.0507	Populations with more seeds are more likely to naturalize
Height (log transformed)	600, 300 - 1075	*z* = -0.486, *P* = 0.627	No effect
Habitation		*z* = 0.566, *P* = 0.571	No effect
Natural vegetation		*z* = -0.371, *P* = 0.711	No effect
Orchard		*z* = -0.003, *P* = 0.998	No effect
Pastoral land		*z* = -0.800, *P* = 0.423	No effect
Plantation		*z* = 0.003, *P* = 0.998	No effect
Rail/Road		*z* = 0.475, *P* = 0.634	No effect
Transformed		*z* = 0.241, *P* = 0.810	No effect
Vacant land		*z* = -0.004, *P*= 0.997	No effect
Management		All populations are unmanaged	
Forest		*z* = 0.003, *P* = 0.998	No effect
Fynbos		*z* = -0.002, *P* = 0.998	No effect
Grassland		*z* = -0.003, *P* = 0.998	No effect
Savanna		*z* = -0.005, *P* = 0.996	No effect
Soil pH	7, 5 - 8	*z* = 2.576, *P* = 0.010	More neutral soils favour naturalization
Soil drainage		*z* = 1.167, *P* = 0.243	No effect

Figure Legends

Figure 1. Ranked bar plot showing the naturalized range sizes of alien plants in South Africa (log scale) with naturalized Proteaceae highlighted in black. The data was derived from the SAPIA database accessed November 2011.

Figure 2. Situations depicting sites where species can and cannot spread. (A) an urbanized setting which shows *Grevillea robusta* in a parking lot with no chance of spread, (B) *Banksia integrifolia* in gardens where plants can spread into natural fynbos, (C) *Hakea salicifolia* hedge with potential to spread into an abandoned orchard. Photographs: Desika Moodley.

Figure 3. Bioclimatic suitability of *H. salicifolia* subsp. *salicifolia* in (a) its native range in Australia with native distribution records, and (b) across its introduced range in South Africa, the inset map depicts all plantings in South Africa. Species status recorded as not found represents historical populations extensively surveyed but with no living plants. Native distribution data was obtained from the Atlas of Living Australia, http://www.ala.org.au and introduced records were sourced from the SAPIA and the Protea Atlas Project databases.

Figure 4. Relationship between the number of seeds in *H. salicifolia* populations and naturalized (n=32) and non-naturalized (n=30) plantings across South Africa (using the full dataset). Box plots display median, 25th and 75th percentiles, and data range. Open circles indicate outliers.

Figure 5. Relationship between the number of seeds in *H. salicifolia* populations and their respective naturalized (n=16) or non-naturalized (n=10) status (using the climate informed dataset). Box plots display median, 25th and 75th percentiles, and data range.

Figure 6. Potential reasons for naturalization in areas mapped as climatically unsuitable. (a) Plants spreading along a disturbed road verge; (b) Hedge planted adjacent to a pine plantation and spreading under the pines; (c) a population planted in a semi-circular manner around a graveyard, with massive recruitment; and (d) a population in climatically unsuitable area with a fixed irrigation system in place.

Figure 1

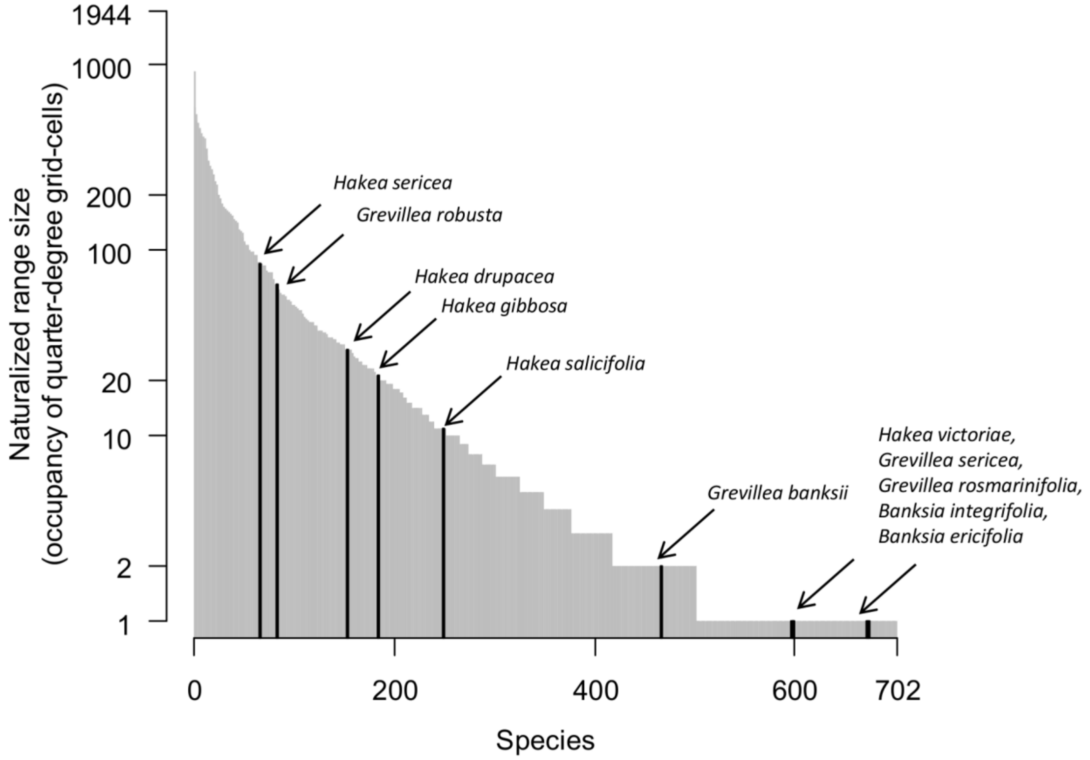

1944
1000
200
100
20
10
2
1
Naturalized range size
(occupancy of quarter-degree grid-cells)
0
200
400
600
702
Species
Hakea sericea
Grevillea robusta
Hakea drupacea
Hakea gibbosa
Hakea salicifolia
Grevillea banksii
Hakea victoriae,
Grevillea sericea,
Grevillea rosmarinifolia,
Banksia integrifolia,
Banksia ericifolia

Figure 2

Figure 3

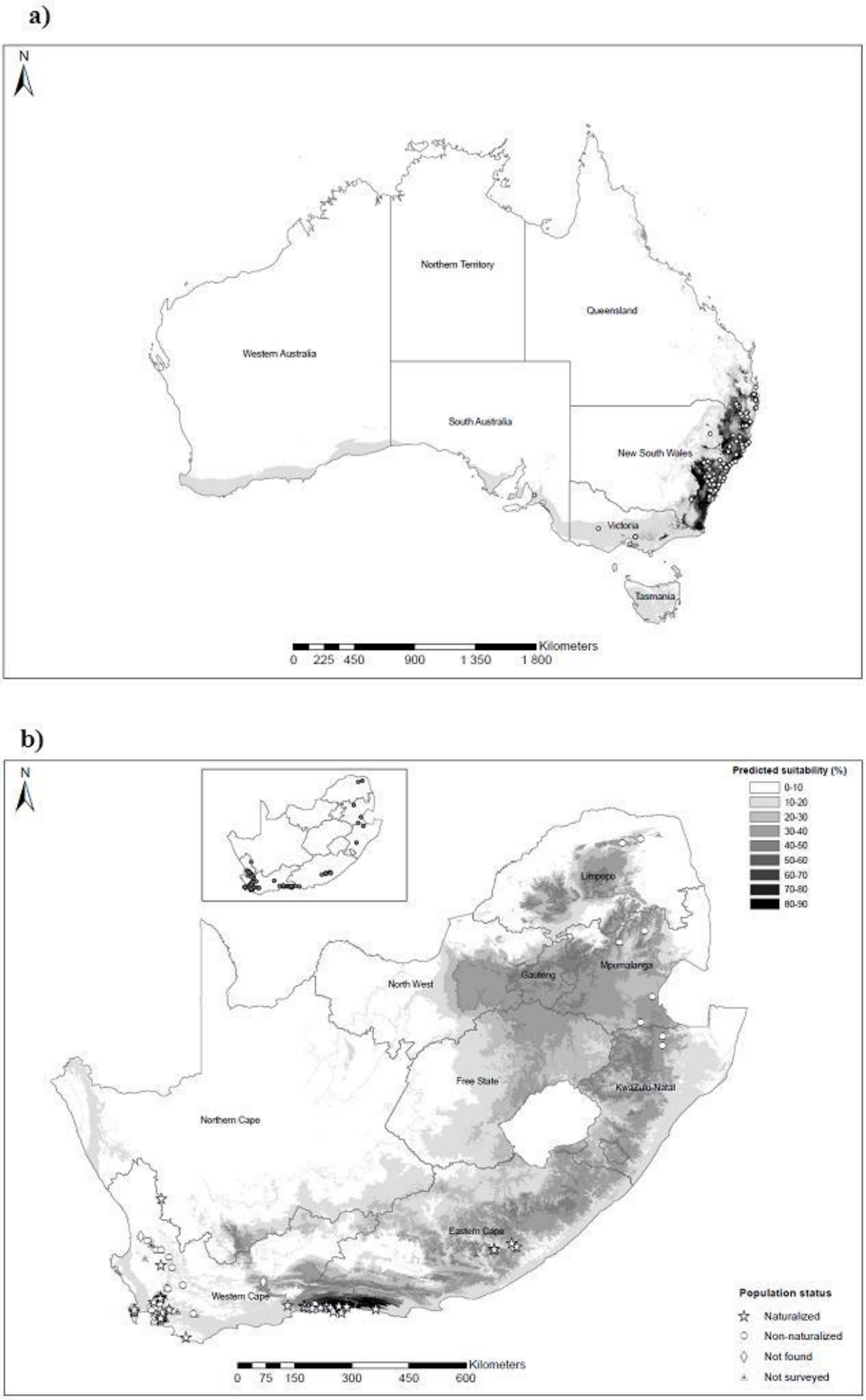

a)
N
Northern Territory
Queensland
Western Australia
South Australia
New South Wales
Victoria
Tasmania
Kilometers
0 225 450 900 1 350 1 800
b)
N
Predicted suitability (%)
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
80-90
Limpopo
Mpumalanga
Gauteng
North West
Free State
KwaZulu-Natal
Northern Cape
Eastern Cape
Western Cape
Population status
☆ Naturalized
○ Non-naturalized
◊ Not found
Not surveyed
Kilometers
0 75 150 300 450 600

Figure 4

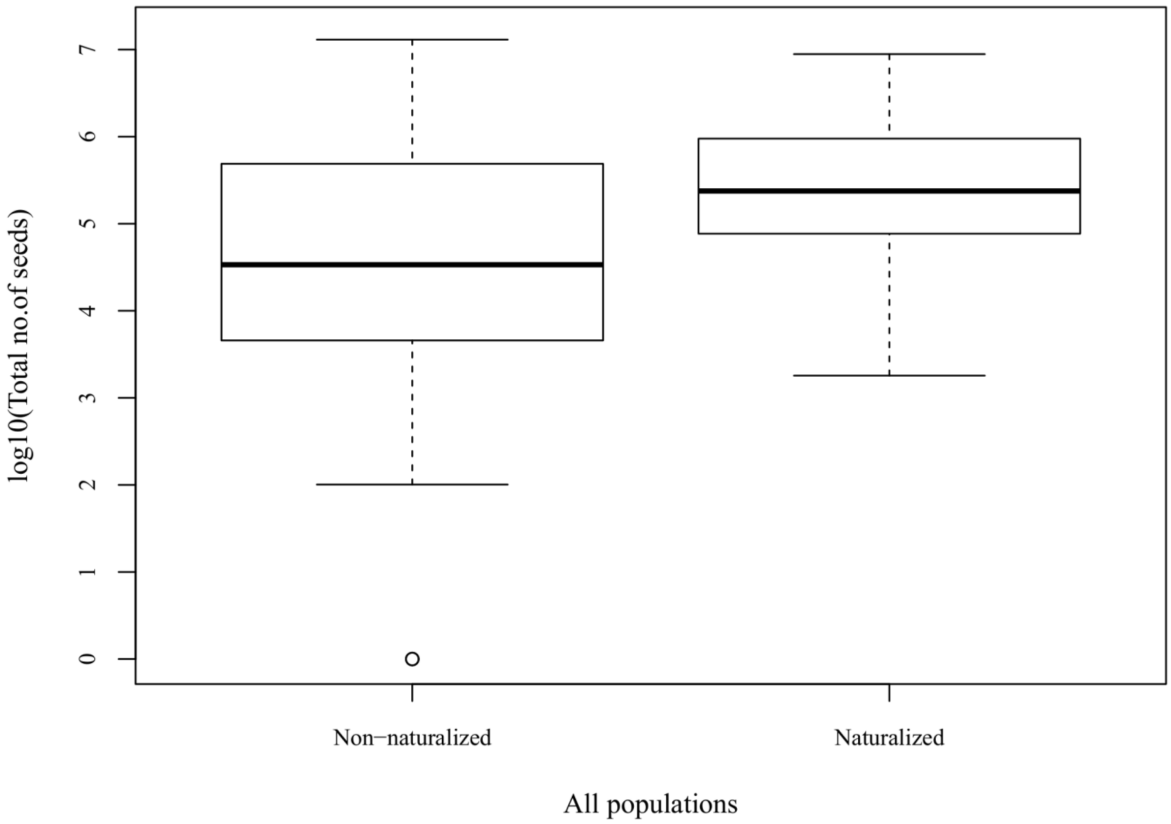

log10(Total no.of seeds)
0
1
2
3
4
5
6
7
Non−naturalized
Naturalized
All populations

Figure 5

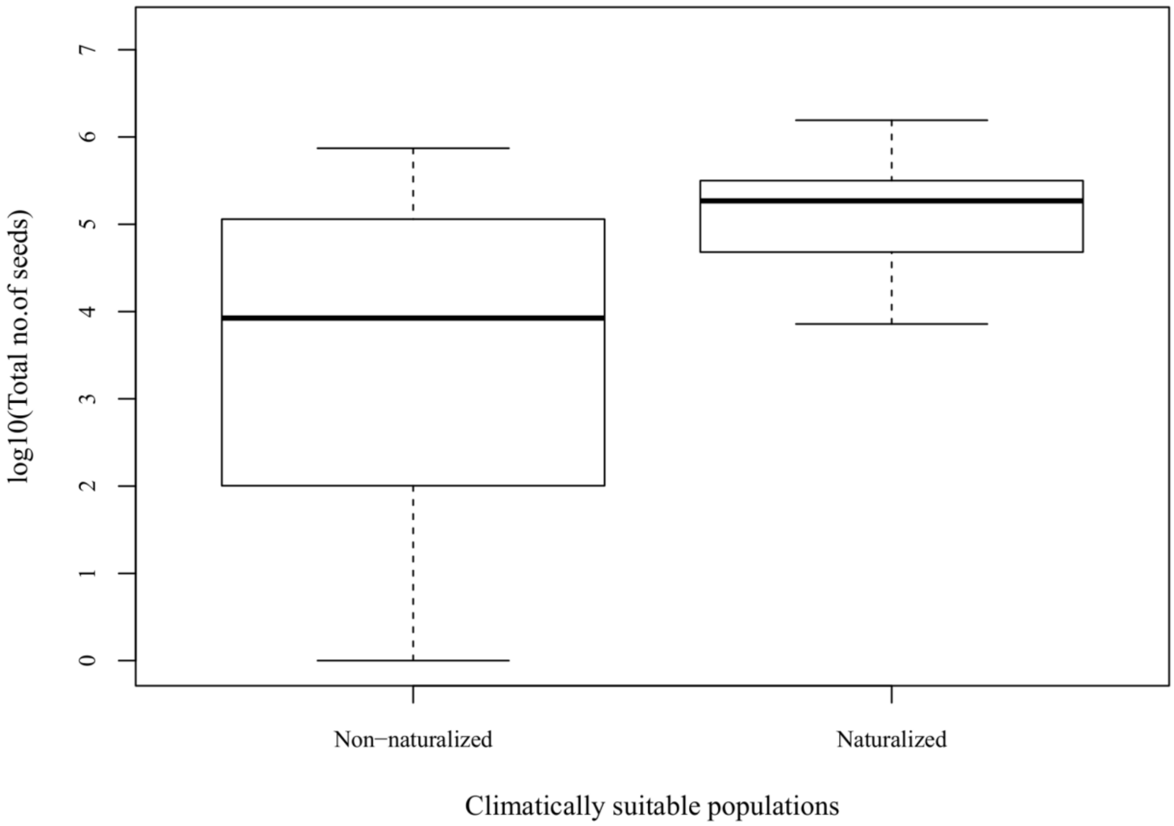
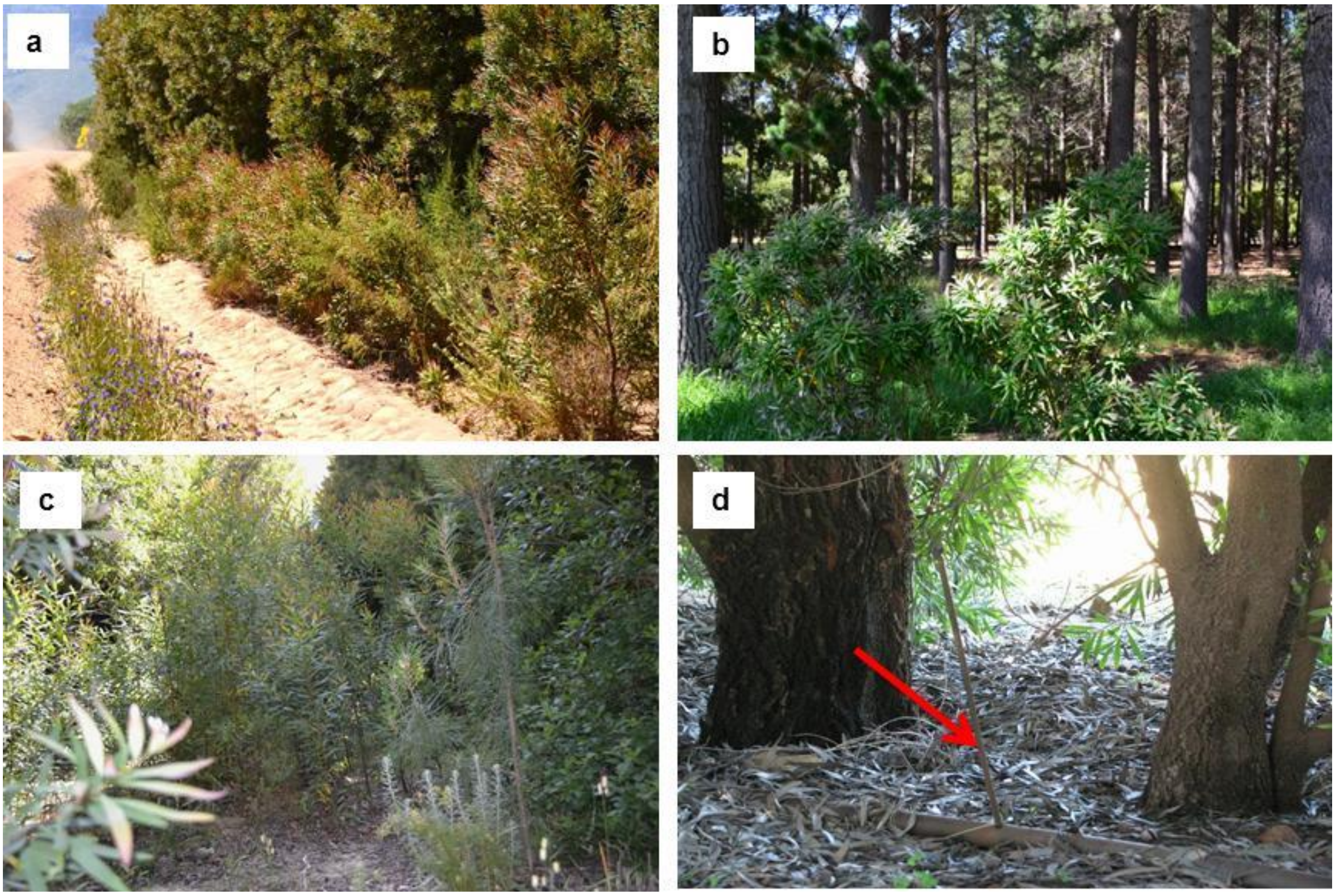

log10(Total no.of seeds)
0
1
2
3
4
5
6
7
Non−naturalized
Naturalized
Climatically suitable populations

Figure 6



Supplementary Tables

Table S1. Summary of the predictive accuracy of *H. salicifolia's* distribution in South Africa.

Model replicate	**AUC**	**TSS**
Mean	0.95	0.822
1	0.956	0.84
2	0.958	0.825
3	0.938	0.82
4	0.948	0.804
Accuracy indicator	**AUC values** (Thuiller et al. 2009)	**TSS values** (Allouche et al. 2006)
Poor	0.5 - 0.7	0 - 0.6
Fair	0.7 - 0.8	
Good	0.8 - 0.9	0.6 -0.8
Excellent	≥ 0.9	≥ 0.8

Table S2. Variable importance of each bioclimatic variable predicted from the generalized boosted model.

Variable	**Contribution**
Mean temperature of the driest quarter (Bio 9)	0.492
Maximum temperature of the hottest month (Bio 5)	0.600
Precipitation of the driest quarter (Bio 17)	0.285

Table S3. Propagule pressure effect between *H. salicifolia* planted in climatically suitable (n=26) and unsuitable (n=36) areas, tested in a generalized linear model.

Coefficients	**Estimate**	**Standard error**	***z* value**	**Pr (>|z|)**
Intercept	-2.70	1.82	-1.48	0.14
log(seed output + 1)	0.21	0.14	1.41	0.16
Suitability	-2.22	3.37	-0.66	0.50
log(seed output + 1) : Suitability	0.29	0.30	0.98	0.32

Supplementary Figure Legends

Figure S1. Matrix plot of pair-wise correlations between the independent predictor variables.

Figure S2. The major land use types of all naturalized and non-naturalized *H. salicifolia* populations. Habitation refers to populations planted in farm yards and gardens, transformed land is dominated by invasive alien plants and vacant land includes areas of open space which was abandoned.

Figure S1

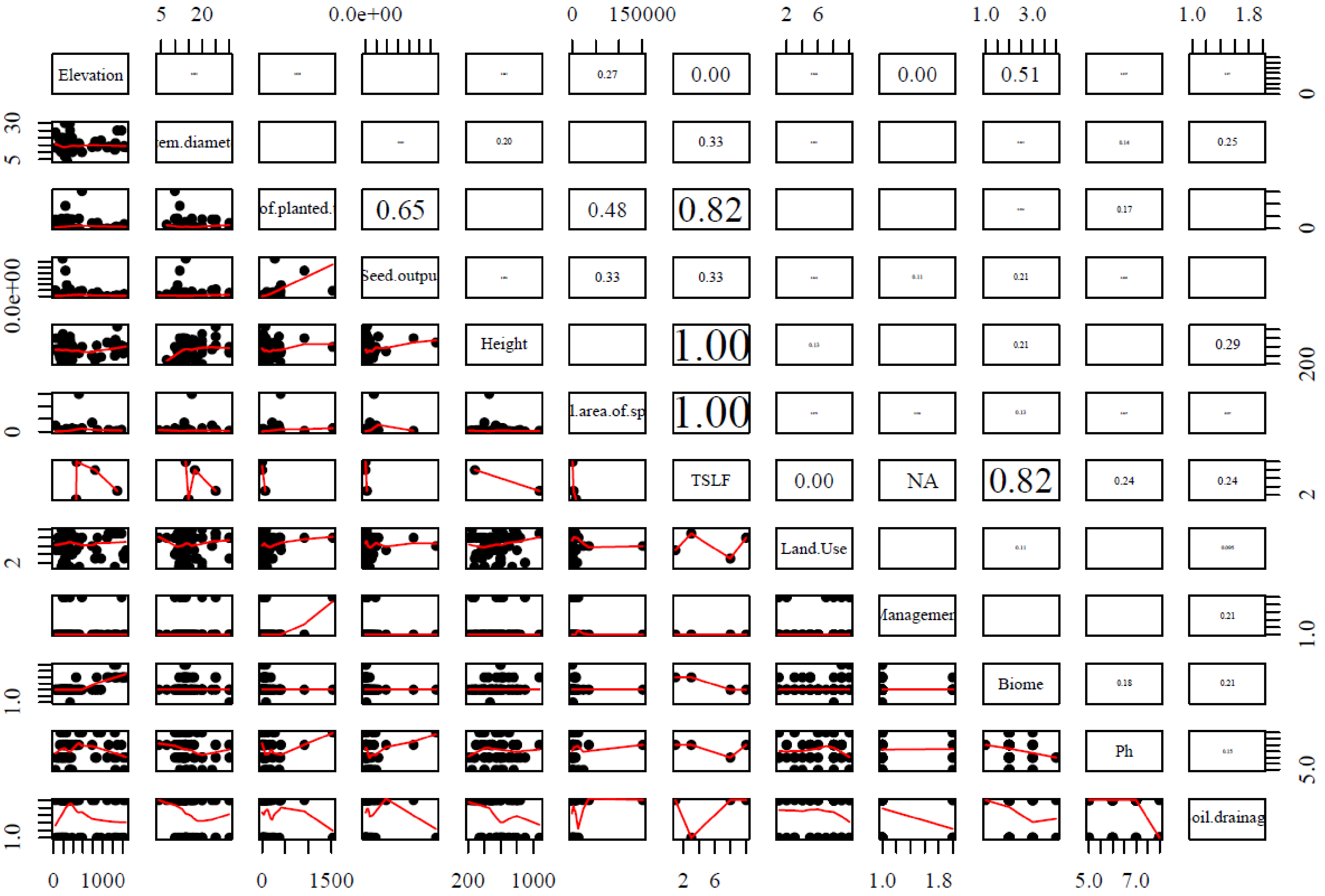
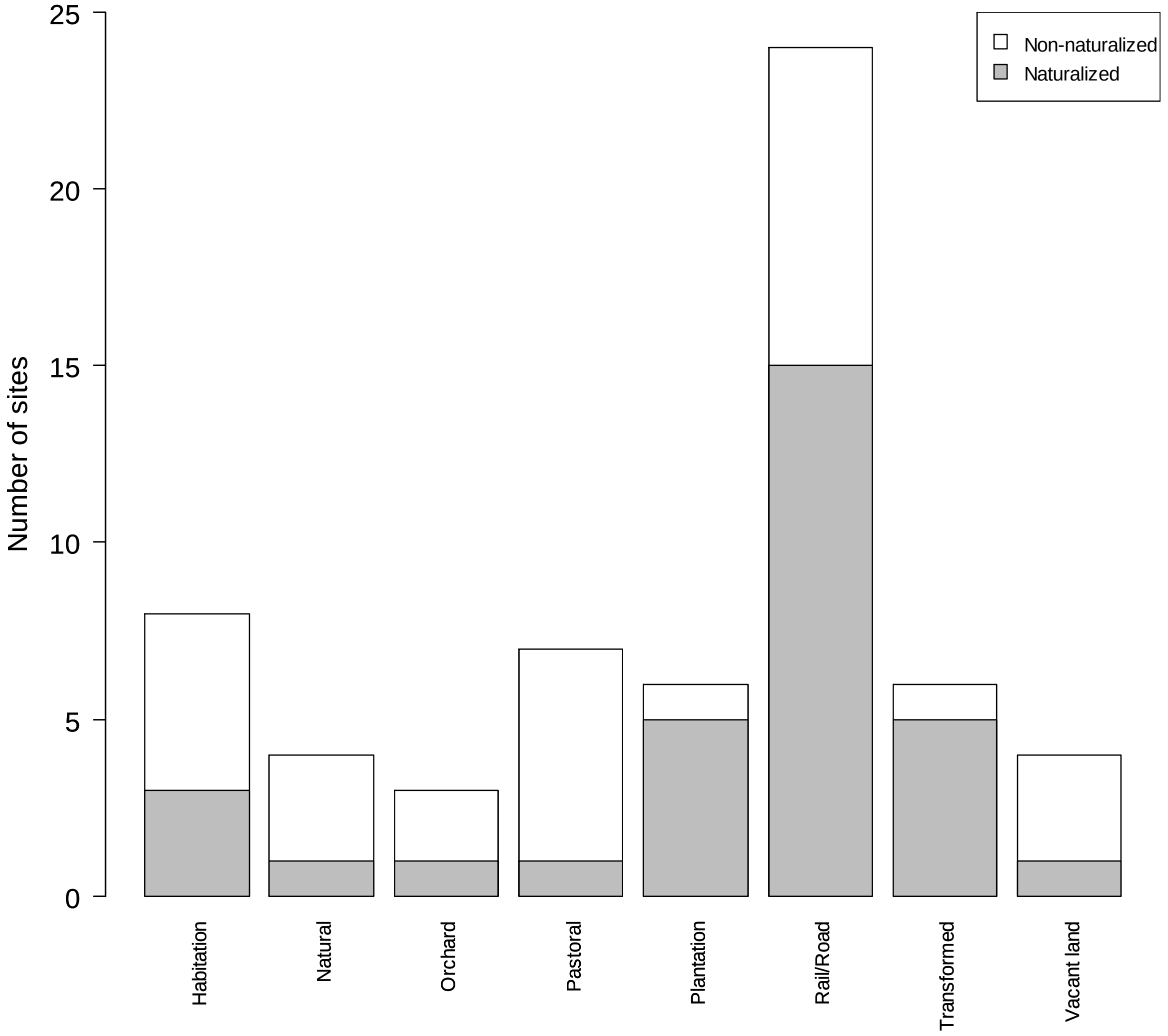

5
20
0.0e+00
0
150000
2
6
1.0
3.0
1.0
1.8
Elevation
0.27
0.00
0.00
0.51
0
30
5
em.diamet
0.20
0.33
0.14
0.25
of.planted.
0.65
0.48
0.82
0.17
0
0.0e+00
Seed.outpu
0.33
0.33
0.11
0.21
Height
1.00
0.13
0.21
0.29
200
0
l.area.of.sp
1.00
0.13
TSLF
0.00
NA
0.82
0.24
0.24
2
2
Land.Use
0.11
Managemen
0.21
1.0
1.0
Biome
0.18
0.21
Ph
0.15
5.0
1.0
oil.drainag
0
1000
0
1500
200
1000
2
6
1.0
1.8
5.0
7.0

Figure S2


Number of sites
0
5
10
15
20
25
☐ Non-naturalized
▨ Naturalized
Habitation
Natural
Orchard
Pastoral
Plantation
Rail/Road
Transformed
Vacant land

Chapter 4: The role of autonomous self-fertilization and pollinators in the early stages of plant invasions: *Hakea* and *Banksia* (Proteaceae) as case studies

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Contribution of each author:

DM & SG: Planning of the study.

DM: Conducted pollination experiments, statistical analyses and led the writing.

SG: Conducted pollination experiments and commented on the manuscript.

DMR: Provided comments on the manuscript.

JRUW: Provided comments on the manuscript and statistical advice.

Intended journal: *South African Journal of Botany*

Abstract

Pollinators often play an important role in facilitating successful plant invasions, but the absence of an appropriate pollinator can limit spread. We examine the role of pollinators for several Proteaceae species introduced from Australia to South Africa. These regions share similar pollinator systems and many species are specialized on particular functional groups (e.g. bees, nectarivorous birds or non-flying mammals); this provides an ideal opportunity to test the role of breeding systems and the importance of pollinators in plant invasions. Many alien tree species are invasive in South Africa, but only 8 out of 24 introduced Proteaceae species are invasive. We investigated whether pollination and autonomous self-fertilization are obstacles for successful invasion (i.e. naturalization and spread) in five *Banksia* and one *Hakea* species. In addition, we conducted pollinator observations and undertook a detailed study on the breeding system of *Hakea salicifolia* comparing natural fruit set to pollen-supplemented, autonomous, hand-selfed and hand-crossed treatments between naturalized and non-naturalized populations. All five *Banksia* species were heavily utilized by native nectar-feeding birds and insects. All *Banksia* species are self-compatible to some extent, but the number of capsules set in four species increased significantly when flowers were open to pollinators. *H. salicifolia* flowers are visited by eleven insect species with the highest visitation incidence by honey bees (*Apis mellifera* subsp. *capensis*). Flowers in naturalized *H. salicifolia* populations received almost four times as many pollinator visits than those in non-naturalized populations. Furthermore, the lower pollinator visitation rate recorded in non-naturalized populations resulted in pollen limitation for the non-naturalized populations [a Pollen limitation Index (PLI) of 0.40] but not for the naturalized populations (PLI ~ 0). Pollen limitation should not prevent invasion since a significant amount of fruits are still produced, however it might reduce the ability of populations to spread. *H. salicifolia* is also capable of autonomous selfing. Our results suggest a limited role of breeding systems in mediating Proteaceae invasions with other factors more important (e.g. features of the recipient environments).

4.1 Introduction

If an introduced species can survive in a new range, a series of barriers determine whether a species will become naturalized and invasive (Blackburn *et al.* 2011), in particular, to successfully reproduce and become invasive, alien plant species must overcome the potential obstacles of mate scarcity and pollinator limitation (Richardson *et al.* 2000b). Mutualisms, such as the interactions between plants and pollinators in the novel range, are fundamental for successful invasion (Richardson *et al.* 2000b; Rodger *et al.* 2010). Plant species that rely on sexual reproduction for population growth and spread need to attract floral visitors, and these visitors need to effectively transfer pollen. A lack of pollinators, or only partly effective pollinators, will result in pollen limitation which could prevent or reduce the establishment and spread of introduced plants (Parker 1997; Richardson *et al.* 2000b).

In regions where pollinators are scarce or absent, plants that are capable of autonomous self-fertilization have a greater chance of naturalizing than self-incompatible species (‘‘Baker’s Law’’; Baker 1965; Harmon-Threatt *et al.* 2009; Rambuda and Johnson 2004; van Kleunen *et al.* 2008; Ward *et al.* 2012). Extending Baker’s idea, self-incompatible species are known to be less invasive while self-compatibility is often associated with invasive success (Hao *et al.* 2011; Rambuda and Johnson 2004; van Kleunen and Johnson 2007b). This is supported by some evidence - self-compatible species do indeed occupy larger novel ranges than self-incompatible species (van Kleunen and Johnson 2007b). However more work is needed to establish the role of uniparental reproduction across various stages of the invasion process. In particular, does uniparental reproduction provide reproductive assurance during naturalization (as originally envisaged by Baker) or is it primarily responsible for altering spread rates by alleviating pollen limitation in small populations at the edge of an invasion front.

Understanding the breeding system of introduced species which have not yet become invasive is important for identifying those that are likely to invade in the future. But studies assessing the importance of pollination and plant-pollinator interactions have focused on species that are already invasive. These species have already overcome the reproduction barrier which confounds attempts to identify whether reproduction is a barrier to invasion (but see Stout *et al.* 2002). Thus it is important to elucidate the role of uniparental reproduction across various stages of plant invasions (Rambuda and Johnson 2004). It would be ideal to test the breeding system within one introduced species that contains populations at different stages in the invasion continuum. This approach specifically addresses whether reproduction limits invasion since there is control over other species-specific traits (e.g. self-compatibility and pollination syndrome).

Proteaceae provides an ideal study group to explore this question. Firstly, Proteaceae show low levels of self-compatibility in their native range (Collins and Spice 1986; Goldingay and Carthew 1998; Goldingay *et al.* 1991; Offord 2004). Limited research has been conducted on the reproductive biology of Proteaceae and results indicate that most species are self-incompatible since there are few or no seeds produced after selfing (Collins and Spice 1986; Horn 1962; Ramsey and Vaughton 1991; Rovere *et al.* 2006; Whelan and Goldingay 1986) and some species that are self-compatible perform better during outcrossing (Carthew *et al.* 1996). Self-incompatible species will therefore depend on pollinators for seed production. Secondly, many Proteaceae are pollinated by only one functional group of pollinators (for example see Collins and Rebelo 1987; Collins 1983; Hanley *et al.* 2009; Rovere *et al.* 2006). Thirdly there are relatively few naturalizing and invasive species and a large number of introduced species globally (chapter 2). Proteaceae is currently underrepresented on the global list of invasive woody plants, probably because most introductions have been very recent (Richardson and Rejmánek 2011), and so there is the possibility to prevent invasions before they occur.

In South Africa, only 8 out of 24 introduced species of Proteaceae are invasive (Protea Atlas Database; Southern African Plant Invaders Atlas (SAPIA); pers. obs.). With the exception of *Grevillea* R.Br. ex Knight, *Hakea* Schrad. & J.C.Wendl., and *Macadamia* F. Muell., most species have been introduced in small numbers to South Africa. Testing selfing capabilities and identifying the role of pollinators for alien species placed at different positions along introduction-naturalization-invasion (INI) continuum will provide a better understanding of the importance of self-fertilization in determining invasiveness. *Banksia* L.f. species introduced into South Africa provides an opportunity to test this since there are species with different invasion status. In addition, *Hakea salicifolia* (Vent.) B.L.Burtt presents a unique opportunity to study the importance of reproduction during the invasion process through a comparison of naturalized and non-naturalized populations.

The goal of this study was to assess the importance of pollinators and autonomous selfing in the early stages of the invasion process by using Proteaceae species introduced into South Africa as a case study. Specifically we aimed to 1) determine the ability of autonomous seed production versus pollinator contribution for five *Banksia* species, across the introduction-naturalization-invasion continuum; and 2) determine whether pollinators and the breeding system of *H. salicifolia* can explain why some populations naturalize and others do not.

4.2 Methods

4.2.1 Study species

4.2.1.1 *Banksia* species

Banksia is a large genus of trees and shrubs consisting of 172 species that are widespread in Australia (George 1999; D. Moodley, unpublished results). At least 11 species have been introduced into South Africa (D. Moodley, unpublished results; Southern African Plant Invaders Atlas, accessed March 2012; Protea Atlas Database, accessed June 2011). The majority of species produce showy inflorescences with copious amounts of nectar to attract birds.(George 1999). Some species are pollinated by insects or mammals (Carpenter 1978; Cunningham 1991). *Banksia* species in South Africa usually set two seeds per capsule, except for *B. formosa* (R.Br.) A.R.Mast & K.R.Thiele (formerly *Dryandra formosa*) which sets one seed per capsule (pers. obs.). Winged seeds are stored in woody follicles which open after fire (serotiny) with some species (ex. *Dryandra* species) releasing seeds upon maturity (George 1999; pers. obs.).

We examined five species in this study. *Banksia coccinea* R.Br. has only been recorded in three sites in South Africa and has not been recorded to naturalize. The studied population in Elim comprised 48 individuals planted for cut flowers and ~3070 seeds are stored in the canopy in veld 6 years old (number of planted individuals and seed bank size was estimated in chapter 3). The second species examined that has not naturalized is *B. speciosa* R.Br. which has been recorded at seven sites. The studied population in Elim contained 29 planted trees for cut flower use and comprised a canopy seed bank of ~37500 seeds in veld 11 years old.

B. formosa (four populations in South Africa) and *B. serrata* L.f. (one population in South Africa) are recorded as naturalized. The *B. formosa* population in Elim selected for this study had 1978 individuals, planted for cut flowers. Seeds are produced in abundance (estimated more than 26 million seeds in the 10 year-old stand) and are released upon maturity (chapter 3; pers. obs.) – a high propagule pressure. A single population of 9 planted *B. serrata* trees in Betty's Bay, planted in natural fynbos, has spread following the last fire with a canopy seed bank of ~180 000 seeds in 14 year old veld.

Lastly, nine *B. integrifolia* L.f. populations have been identified of which at least one population, at Pringle Bay, is invasive. This population was selected for our pollination experiment. From a single tree planted 32 years ago, the population currently covers approximately 39000 m^2 with a canopy stored seed bank of ~ 750 000 seeds.

4.2.1.2 *Hakea salicifolia*

Hakea salicifolia is a large bushy shrub or small tree (Barker *et al.* 1999) native to south-east Queensland and eastern New South Wales in Australia. It has naturalized in several regions of the world (Barker *et al.* 1999; Southern Africa Plant Invaders Atlas, accessed March 2012; Delivering Alien Invasive Species Inventories for Europe, www.europe-aliens.org, accessed November 2011; Randall 2007; Williams 1992), including South Africa where it was introduced around 1830 and is now widely used as an ornamental or hedge plant (Le Maitre *et al.* 2008). This species has recently been identified as naturalizing in some sites, but not in others (D. Moodley, chapter 3). Of the 113 populations that were recorded in South Africa, 32 populations have naturalized (D. Moodley, chapter 3).

The scented white flowers form dense clusters in the leaf axils. In Australia *H. salicifolia* flowers between August and November (Barker *et al.* 1999), with similar duration in South Africa. Species belonging to the *Hakea* genus are visited by bees and wasps in their native range (Armstrong 1979) which is a relatively unspecialized pollination syndrome. This is followed by the development of two winged seeds enclosed in woody follicles (Barker *et al.* 1999). The wind dispersed seeds are released following fires. Seed viability is generally high in *Hakea*, irrespective of follicle age (Richardson *et al.* 1987). However seed viability declines in old *H. salicifolia* follicles (Richardson *et al.* 1987).

4.2.2 Study sites

This study was conducted in the Western Cape region where most populations of *Hakea salicifolia* are planted and where all known *Banksia* plantings occur (Table S1). *H. salicifolia* sites were selected according to previously classified naturalized and non-naturalized populations (D. Moodley, chapter 3). This comprised 8 naturalized and 8 non-naturalized populations. One *B. coccinea* and a *B. speciosa* population were selected as casual sites; one *B. serrata* population in Betty's Bay and one *B. formosa* population comprise naturalized sites; and one *B. integrifolia* population characterizes a species which has become invasive in at least one site.

4.2.3 Floral visitors

To determine whether pollinators visited these novel food sources we observed and scored visits as legitimate when there was contact with anthers or stigma. Prior to observing visitors, all inflorescences visible from the observation post were recorded. For each observation period, the identity of all pollinator species and the number of inflorescences visited were recorded. Pollinator visitation rates were quantified as the number of visits per inflorescence per hour.

Starting in the morning we observed 30 inflorescences for 150 minutes over two days for *B. speciosa* (90 minutes on 12 July 2011; 60 minutes on 14 July 2011). One hundred and eighty five *B. integrifolia* inflorescences were observed for 520 minutes over two days (205 minutes on 20 July 2011; 315 minutes on 22 July 2011). The days we chose were sunny throughout the observation period, however strong winds could not be avoided at the *B. integrifolia* site.

For *H. salicifolia*, we conducted 83 minutes of observations on 1650 inflorescences in two naturalized populations (23 minutes on 27 September 2012; 60 minutes on 5 October 2012) and 207 minutes of observations on 3100 inflorescences in four non-naturalized populations (48 minutes on 28 September 2012; 60 minutes on 5 October 2012; 50 minutes on 5 October 2012; 49 minutes on 5 October 2012) over a three-day period.

4.2.4 Breeding systems

To assess whether pollinators are important for reproduction in the introduced range, pollinator exclusion experiments were conducted to examine autonomous seed production. Pollen supplementation experiments were conducted to assess the effectiveness of pollinators and to determine whether pollen limitation restricts invasion.

4.2.4.1 *Banksia* species

The experimental design for *Banksia* species involved randomly assigning inflorescences to an open or bagged treatment. The bagged treatment (Figure 2a) consisted of bagging inflorescences that were still in bud phase using fine-mesh nylon bags. These bags prevent potential pollinators from accessing the inflorescences but are permeable to air and moisture. The open treatment (Figure 2b) served as the control, whereby inflorescences were tagged at the base and left open for pollination. Each pair of open and bagged treatments was performed on different plants.

4.2.4.2 *Hakea salicifolia*

Experiments were conducted for 8 naturalized and 8 non-naturalized populations. Each population comprised between six to nine treated individuals. Branches with flowers that were still in bud stage were randomly selected, with each plant comprising a set of five treatments. Each treatment was performed on a different branch. The treatments comprised natural, pollen supplementation, autonomous, bagged hand-crossed and hand-selfed flowers. Prior to blooming we visited all populations and tagged two branches (for the natural and pollen supplementation experiments) and bagged three branches (for the autonomous, hand-selfed and hand-crossed treatments) on each plant. Branches were bagged with fine-mesh nylon bags to exclude potential pollinators. “Natural” treatments: flowers were left open to pollinators; “pollen supplementation” treatments: open flowers were augmented with hand pollination using pollen from donor plants located at least five metres away; “autonomous” treatments: bagged flowers were left un-manipulated; “hand-crossed” treatments: bagged flowers were hand pollinated with pollen from donor plants located at least 5 metres away and carefully re-bagged; “hand-selfed” treatments: bagged flowers were hand pollinated with pollen from other flowers of the same plant and carefully re-bagged. Hand pollination treatments involved gently rubbing pollen from one stigma onto another using tweezers. We documented the number of flowers for all treatments in order to measure the proportion of fruit set (number of fruits produced/number of flowers). All branches were harvested four weeks later. In total we treated 7754 flowers on 127 plants for the open treatment, 1857 flowers on 127 plants for pollen supplementation, 6732 flowers on 126 plants for the autonomous treatment, 1390 flowers on 126 plants for the hand-crossed treatment and 1305 on 126 plants for the hand-selfed treatment. To ensure that fruits produced two seeds, we dissected 1896 fruits (at most three fruits per treated plant). Since all dissected fruits contained two seeds, we only worked with the number of fruits produced.

4.2.5 Data analysis

For each *Banksia* species, we used a generalized linear model with Poisson error to determine whether natural and autonomous treatments differed in the number of capsules set per inflorescence.

To test for differences in fruit production between *H. salicifolia* populations and between the five treatments, we fitted a generalized linear mixed-effect model (GLMM) with a binomial error structure using the ‘lme4’ package (Bates *et al.* 2012). Because we treated several flowers on each plant and several plants within each population we used plant identity nested within population identity as a random effect in the GLMM. In order to assess the reproductive fitness of *H. salicifolia* a GLMM was constructed with successful fruit production as the response variable and an interaction between reproductive treatments (5 levels) and population status (naturalized or non-naturalized) as predictor variables. We then compared this model with the model without population status using an analysis of variance (ANOVA) to determine whether reproductive fitness differs between naturalized and non-naturalized populations. We also estimated pollen limitation for naturalized and non-naturalized populations using the Pollen Limitation Index (PLI) proposed by Larson and Barret (2000). This involves calculating the average proportion of fruit set in each treatment for the sixteen populations. The data were then used to calculate the PLI: [1-(natural fruit set/pollen supplementation fruit set)]. All statistical analyses were conducted using R (R Development Core Team 2012).

4.3 Results

4.3.1 Visitor observations

All *Banksia* species were heavily utilized by native nectar-feeding birds and insects. *Banksia speciosa* and *B. integrifolia* were mostly visited by several nectar-feeding birds as well as honey bees (Table 1). The total visit per inflorescence per hour for *B. speciosa* was 0.34 and 0.02 visits per inflorescence per hour was observed for *B. integrifolia*.

Hakea salicifolia flowers were visited by 11 insect species, with similar species present at naturalized and non-naturalized populations (Table 2). Inflorescences are visited by bees, wasps, flies and beetles with honey bees (*Apis mellifera* subsp. *capensis* Esch.) being the most frequent visitors across all sites. In total, inflorescences in naturalized populations (0.15 visits per inflorescence per hour) were visited more frequently than in non-naturalized populations (0.04 visits per inflorescence per hour) but this was not driven by a particular pollinator species (Table 2).

4.3.2 Breeding systems

4.3.2.1 *Banksia* species

Autonomous selfing in *Banksia* species is not related to invasion status, and high levels of autonomous seed production were found in casual, naturalized and invasive species (Figure 2). The number of capsules that set seed between the two treatments was significantly different for *B. coccinea* ($z = 7.57$, $P < 0.05$), *B. serrata* ($z = 15.09$, $P < 0.05$), *B. formosa* ($z = 11.46$, $P < 0.05$) and *B. integrifolia* ($z = 17.98$, $P < 0.05$). However, the number of capsules that set seed was similar between bagged and open treatments for *B. speciosa* ($z = 0.89$, $P = 0.38$). Naturalized species set significantly fewer capsules in the bagged treatments. *Banksia formosa* produced 1 capsule (median; 95%CI: 1.41-6.18) per inflorescence autonomously and 16 capsules (13.60-19.10) naturally. *Banksia serrata* also produced 1 capsule (1.28-6.31) autonomously and 23 capsules (20.18-32.98) naturally. The invasive *B. integrifolia* population produced the greatest number of capsules in both treatments with 108 capsules (99.12-146.28) produced naturally and 46 capsules (38.84-80.55) autonomously.

4.3.2.2 *Hakea salicifolia*

Overall, *Hakea salicifolia* produced similar numbers of fruit naturally and autonomously, but pollen supplementation significantly enhanced fruit production (Table 3 & S2). Furthermore, the number of fruits successfully produced in all pollination treatments revealed a significant treatment effect (Table 4a). However, there was no significant difference for each treatment when compared between naturalized and non-naturalized populations (df = 5, $\chi^2 = 4.88$, $P = 0.43$; Table 4b). This suggests that fruit production does not affect the status of *H. salicifolia* populations.

Although there was no significant difference between naturalized and non-naturalized populations, on average more fruit is produced when pollen is added to flowers compared to fruit produced naturally (Table 3). Furthermore, this is potentially driven by non-naturalized populations since fruit set increased by more than 70% when pollen was added (Table 3). The low fruit set resulted in many zero's, which might mask some of the differences.

The Pollen Limitation Index for all populations was 0.22 which confirms pollen limitation in *H. salicifolia*. A value of zero indicates no pollen limitation, but in the case of *H. salicifolia* 22% fruits were not produced because of a lack of pollen. Furthermore, pollen limitation was high in non-naturalized populations (PLI of 0.40) while no pollen limitation was identified in naturalized populations (PLI ~ 0). This is supported by the hand-crossed treatments which produced significantly more fruits than the natural ($P < 0.05$) and autonomous ($P < 0.05$) treatments (Table S2).

4.4 Discussion

Differences in levels of autonomous self-pollination in naturalized and non-naturalized populations are not significant and thus cannot explain the invasion dynamics of introduced Proteaceae species in South Africa. The results suggest that autonomous seed production is not preventing any of the *Banksia* species from producing fruit and should not prevent *H. salicifolia* populations from naturalizing. In its native range, *B. coccinea* and *B. formosa* have low levels of self-compatibility (Fuss and Sedgley 1991; Matthews and Sedgley 1998), however pollination systems of the other studied species have not been evaluated. In South Africa, all studied species demonstrated some degree of self-compatibility.

This is one of the very few detailed studies that explore the importance of pollinators and breeding system at the early stages of plant invasion (Stout *et al.* 2002; van Kleunen *et al.* 2008). Most studies assess the importance of reproductive fitness in species that have already overcome reproductive barriers (Rodger *et al.* 2010; Ward *et al.* 2012). High reproductive fitness is commonly associated with invasiveness, although a low level of self-compatibility is not (Baker 1965; Lloret *et al.* 2005; Rambuda and Johnson 2004; van Kleunen *et al.* 2008). Therefore, it should be easier for self-compatible species to invade novel ranges because autonomy offers reproductive assurance (van Kleunen and Johnson 2007b). We established that birds and insect pollinators play an important role in the reproductive performance of Proteaceae, especially for *Banksia* species.

In its native range *Banksia* species are served by several nectar-feeding bird species, insects, marsupials and rodents (Collins and Rebelo 1987), and they co-opt sunbirds, sugarbirds and honey bees in South Africa. In South Africa, these species show higher seed set in the presence of these pollinators. Therefore, these species require pollinators for enhanced seed production. Naturalized *Banksia* species showed more reliance on pollinators and although pollinators enhanced seed set of the invasive species, *B. integrifolia* demonstrated higher selfing capabilities. This provides support for Baker's law (Baker 1955) which states that establishment is more likely for self-fertilizing species and also supports studies showing that pollinators can improve seed production in self-fertilizing invasive species (Geerts and Pauw 2009; Rodger *et al.* 2010). Alien plant species are rarely limited by pollinators because many widely recognized invasive plants are well integrated into pollination networks in their introduced range (Morales and Aizen 2006; Olesen *et al.* 2002). However if these *Banksia* species are introduced to regions without nectar-feeding birds, we would expect seed production to be lower and the chance of invasion to be significantly less (see Ollerton *et al.* 2012 for regions with no specialized nectar feeders).

Flowers of *Hakea salicifolia* are not specialized and many different pollinators visited this species. The ability of plants to attract suitable pollinators that are efficient in transferring pollen determines reproductive success (Richardson *et al.* 2000b). *H. salicifolia* is able to produce fruit autonomously but pollinator visits slightly enhanced fruit production (Table 3). Honey bees were the most frequent visitors to *H. salicifolia* inflorescences, therefore visitation rate can be attributed to their presence (i.e. 59% of visits were made by honey bees). Moreover, reproduction will be maintained in regions where this generalist pollinator is present (Rodger *et al.* 2010). We found non-naturalized populations to be pollen limited. Pollen limitation can result if pollinator visits are low due to Allee effects, such as low fitness due to small population sizes which reduces pollinator visits (Davis *et al.* 2004). In addition, pollen quantity may be limiting when plants compete for the services of pollinators (i.e. Allee effects; Cappuccino 2004; Groom 1998).

Pollinator visitation rates are more than three times higher in naturalized *H. salicifolia* sites than non-naturalized populations. Thus, pollinators are effective in naturalized sites, but occur in low abundances in non-naturalized populations, potentially explaining the pollen limitation. In addition, hand-selfing partially alleviates pollen limitation in non-naturalized populations. The two naturalized populations were surrounded by vineyards and orchards whereas the four non-naturalized populations where planted close to a vineyard, along a road, in pastoral land, and along an old orchard. The presence of many fruit trees increases the number of insect visitors and this probably explains why populations surrounded by fruit trees have more visitors. However, pollen limitation may not restrict non-naturalized *H. salicifolia* populations from spreading but could partly explain why some populations have not yet naturalized. For example, the rate of spread in *Cytisus scoparius* was reduced due to pollen limitation, but this species is highly invasive (Parker 1997).

Studies on other invasive plant species have demonstrated that self-compatibility and suitable pollinators in the introduced range are important for successful invasions (Pyšek et al. 2011; Rambuda and Johnson 2004; Rodger et al. 2010; van Kleunen and Johnson 2005, 2007a; van Kleunen et al. 2008; Ward and Johnson 2012). Our study adds to the sparse literature on self-compatibility in invasive woody species. More importantly, determining reproductive traits that confer invasiveness are crucial for understanding the drivers of invasions (Rambuda and Johnson 2004). Ideally, comparisons conducted within one species (i.e. between naturalized and non-naturalized populations) could provide better insights into determinants of invasiveness. This robust test enabled us to demonstrate that autonomous self-pollination in *Banksia* and *Hakea* does not limit the spread of invasive species, as originally proposed by Baker, because these species are self-compatible but occupy different positions along the INI continuum. We were also able to show that non-naturalized *H. salicifolia* populations have lower pollinator visitation rates which results in pollen limitation. However, pollinator limitation may slow down seed production but will not restrict spread in the future (Richardson *et al.* 2000b; Traveset and Richardson 2006).

4.5 Conclusion

Banksia species are pollinated by nectar-feeding honey birds in their native range and this is maintained by sugarbirds, sunbirds and honey bees in South Africa. While *Banksia* species demonstrate high selfing capabilities, pollinators are important in the introduced range. Pollinators in South Africa are also maintaining reproductive success of *Hakea salicifolia,* but they are not very effective because autonomous seed production is similar to natural seed set. In this study we found that pollinators and breeding systems are unlikely to explain differences in the degree of invasion success, because naturalized and non-naturalized *H. salicifolia* populations exhibit similar reproductive performance. Moreover, it is unlikely for alien Proteaceae in South Africa to be restricted by pollination since species either produce large amounts of seeds autonomously or are visited by an array of pollinators. Our results do not show a strong role of reproduction in explaining plant invasions but points to invasibility characteristics driving invasions (i.e. land use types). Therefore, we recommend that more studies should assess the breeding system of alien species that comprise populations with different invasion status in order to determine the role of reproduction in plant invasions.

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Tables

Table 1. Visitation rates of different groups of inflorescence visitors to *Banksia speciosa* and *B. integrifolia* in the Western Cape, South Africa.

Species	**Visits per inflorescence per hour**	
	B. speciosa	*B. integrifolia*
Apis mellifera subsp. *capensis*	0.1200	0.0118
Promerops cafer (Cape Sugarbird)	0.0267	0.0100
Zosterops pallidus (Cape White-eye)	0	0.0025
Cinnyris chalybeus (Lesser Double-collared Sunbird)	0.0800	0.0031
Nectarinia famosa (Malachite Sunbird)	0.1200	0
Total	0.3467	0.0274

Table 2. Floral visitors and visitation rates at naturalized and non-naturalized *Hakea salicifolia* populations planted in the Western Cape, South Africa. Pollinator importance is ordered according to decreasing visitation rates (i.e. combined visitation rate of naturalized and non-naturalized sites).

Species	**Visits per inflorescence per hour**	
	Naturalized	Non-naturalized
Apis mellifera subsp. *capensis*	0.0858	0.0309
Scathophaga stercoraria	0.042	0.001
Asarkina africana	0.0065	0.0031
Polistes fastidiosus	0.0042	0.0016
Eristalinus taeniops	0.0042	0.0003
Musca domestica	0.0033	0.0009
Dejeania bombylans	0.0042	0
Chrysomya marginalis	0.0023	0.0017
Chrysomya albiceps	0.0014	0.0014
Phytomia incisa	0	0.0011
Cardiotarsus acuminatus	0.0005	0
Total	0.1543	0.0421

Table 3. Average fruit set (the proportion of flowers producing fruit) in *Hakea salicifolia* populations in the Western Cape, South Africa, assigned to five pollination treatments.

Treatment	**Proportion fruit set per flower Mean (range)**		**Fruit set across all sites**
	Naturalized sites	Non-naturalized sites	**Mean (range)**
Natural	0.051 (0-0.546)	0.040 (0-0.375)	0.046 (0-0.546)
Autonomous	0.023 (0-0.500)	0.030 (0-0.786)	0.027 (0-0.786)
Pollen added	0.051 (0-0.600)	0.069 (0-0.800)	0.060 (0-0.800)
Cross	0.031 (0-0.272)	0.062 (0-0.750)	0.047 (0-0.750)
Self	0.030 (0-0.286)	0.044 (0-0.363)	0.037 (0-0.363)

Table 4. Results of the GLMM with a binomial error structure for *H.salicifolia* populations in the Western Cape, South Africa. a) The effect of successful fruit production in all treatments. b) The interaction effect between the treatments (5 levels) and naturalized and non-naturalized populations.

a) Formula: *Success_Failure* ~ *Treatment* + (1| *Population_No/Plant_No*)

Family: binomial

AIC: 733.7

Random effects

Groups	Variance	Std.Dev.
Plant_No: Population_No	0.56	0.75
Population_No	1.01	1.00

Fixed effects

	Estimate	Std. Error	z value	Pr(>|z|)
Natural	0.65	0.32	2.00	0.04
Autonomous	-0.69	0.29	-2.40	0.01
Pollen added	-1.41	0.29	-4.87	< 0.05
Cross	-1.97	0.30	-6.47	< 0.05
Self	-2.01	0.30	-6.60	< 0.05

b) Formula: *Success_Failure* ~ *Treatment* * *Population_status* + (1| *Population_No*/*Plant_No*)

Family: binomial

AIC: 752.9

Random effects

Groups	Variance	Std.Dev.
Plant_No: Population_No	0.57	0.76
Population_No	1.08	1.04

Fixed effects

	Estimate	Std. Error	z value	Pr(>|z|)
Natural	0.989	0.481	2.056	0.040
Autonomous	-1.181	0.427	-2.765	0.006
Pollen added	-1.945	0.443	-4.388	< 0.05
Cross	-2.575	0.471	-5.468	< 0.05
Self	-2.693	0.477	-5.641	< 0.05
Natural x status	-0.624	0.665	-0.937	0.349
Autonomous x status	0.921	0.577	1.595	0.111
Pollen added x status	0.970	0.590	1.643	0.100
Cross x status	1.096	0.619	1.770	0.077
Self x status	1.214	0.624	1.946	0.052

Figure Legends

Figure 1. Plate illustrating a (a) bagged *Banksia integrifolia* inflorescence; (b) tagged *B. formosa* branch; (c) pollen addition on a *B. coccinea* inflorescence; (d) Honey bee (*Apis mellifera* subsp. *capensis*) feeding on a *H. salicifolia* inflorescence; (e) Cape Sugarbird (*Promerops cafer*) feeding on a *B. speciosa* inflorescence; and (f) *B. serrata* branch with a massive canopy stored seed bank. Photographs: Sjirk Geerts and Desika Moodley

Figure 2. Open control versus bagged seed production in two casual (*Banksia speciosa* & *B. coccinea*), two naturalized (*B. formosa* & *B. serrata*) and one invasive (*B. integrifolia*) *Banksia* species, in the western Cape, South Africa. Comparison of the number of capsules produced between open pollination (*B. coccinea*, n=27; *B. speciosa*, n=18; *B. formosa*, n=20; *B. serrata*, n=19; and *B. integrifolia*, n=20) and bagged treatments (*B. coccinea*, n=27; *B. speciosa*, n=19; *B. formosa*, n=20; *B. serrata*, n=18; and *B. integrifolia*, n=14) was tested for each species. All species produced significantly more capsules in the open pollination treatment, except for *B. speciosa*. Boxplots display the median with a solid line, 25th and 75th percentiles in the lower and upper boxes respectively, and the data range is indicated by the whiskers. Open circles indicate outliers (values more than 1.5 times interquartile distance below 25th percentile).

Figure 1

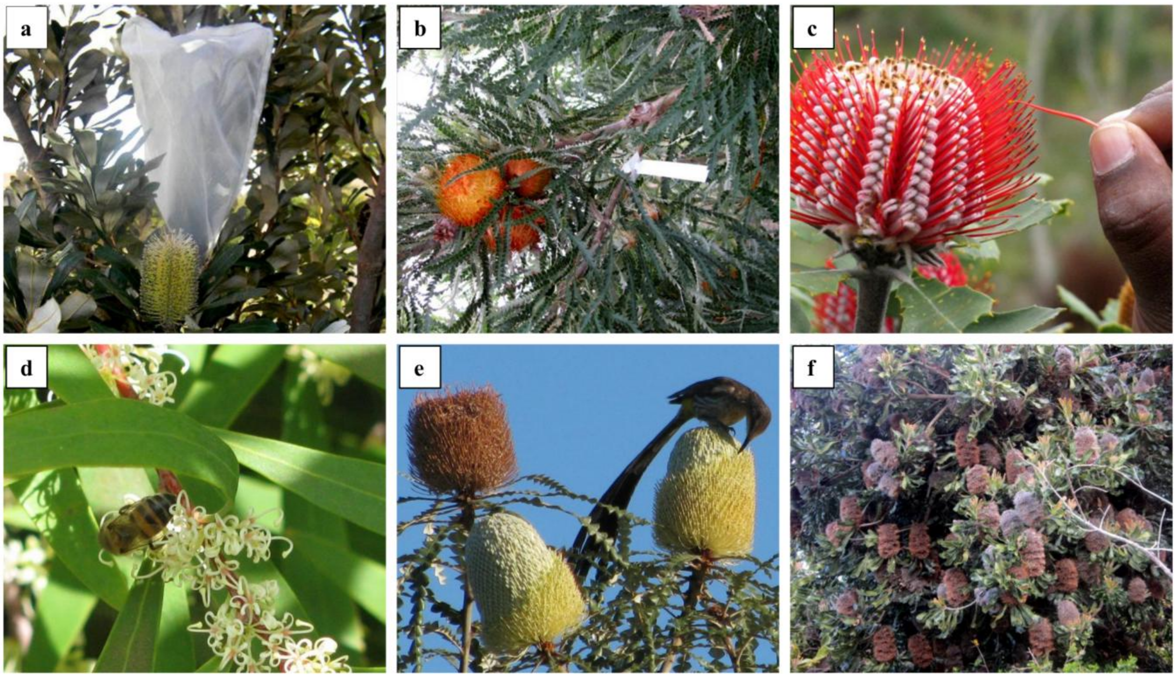
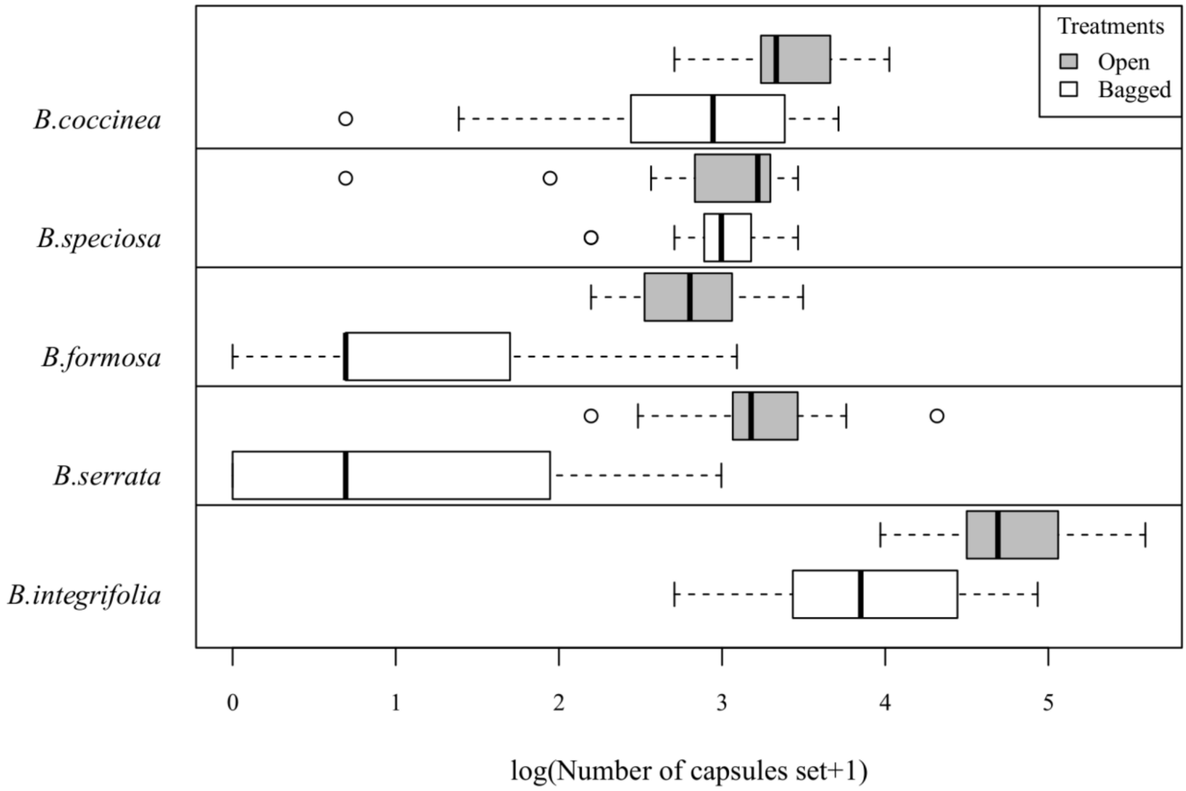


Figure 2


Treatments
Open
Bagged
B.coccinea
B.speciosa
B.formosa
B.serrata
B.integrifolia
0
1
2
3
4
5
log(Number of capsules set+1)

Supplementary Tables

Table S1. Locality details and number of self-sown alien Proteaceae Western Cape where pollination experiments were conducted.

Species	**Locality**	**Latitude**	**Longitude**	**No. of seedlings**	**No. of juveniles**	**No. of mature plants**	**Area covered (m^2)**	**Population status** [1]
Banksia speciosa	Blomkloof farm	-34.5376	19.8433	1	0	0	1842	Casual
B. coccinea	Blomkloof farm	-34.6412	19.7076	0	0	0	NA	Casual
B. formosa	Blomkloof farm	-34.5259	19.8124	27100	6429	9989	19781	Naturalized
B. serrata	Bettys Bay	-34.3506	18.9213	10	34	11	2440	Naturalized
B. integrifolia	Pringle Bay	-34.3532	18.8192	68	183	117	39355	Invasive
Hakea salicifolia	Grabouw	-34.2108	19.0433	103	44	16	608	Naturalized
H. salicifolia	Tokai	-34.0609	18.4270	1611	29	1	23842	Naturalized
H. salicifolia	Paarl	-33.7331	19.0425	4304	910	38	2844	Naturalized
H. salicifolia	Grabouw	-34.1761	19.0758	1693	135	30	2519	Naturalized
H. salicifolia	Paarl	-33.7508	19.0376	2439	787	1	2296	Naturalized
H. salicifolia	Klapmuts	-33.8336	18.8775	47	47	828	2367	Naturalized
H. salicifolia	Theewaterskloof	-34.0171	19.2419	45786	1886	10	6017	Naturalized
H. salicifolia	Grabouw	-34.0749	19.0788	5081	4035	48	13000	Naturalized
H. salicifolia	Theewaterskloof	-34.0183	19.2373	12	12	0	604	Non-naturalized
H. salicifolia	Citrusdal	-32.6101	18.9377	1	0	0	13186	Non-naturalized
H. salicifolia	Grabouw	-34.1595	19.0320	66	131	0	1232	Non-naturalized
H. salicifolia	Romansrivier (near Wolseley)	-33.4933	19.1905	0	0	0	NA	Non-naturalized
H. salicifolia	Paarl	-33.7343	19.0244	0	0	0	NA	Non-naturalized
H. salicifolia	Stellenbosch	-33.9939	18.8270	0	0	0	NA	Non-naturalized

H. salicifolia	Lynedoch	-33.9653	18.7971	0	0	0	NA	Non-naturalized
H. salicifolia	Jonkershoek	-33.9600	18.9158	39	1	0	94	Non-naturalized

[1] Population status classified according to Pyšek et al. (2004) and Richardson et al. (2000a). Casual species do not form self-replacing populations and rely on repeated introductions for their persistence; naturalized species produce self-sown offspring that reproduce consistently without direct human intervention; and invasive species are a subset of naturalized species that produce offspring at a considerable distance from the parent plant (>100 m over <50 years for taxa spreading by propagules; >6 m over 3 years for taxa spreading by roots, rhizomes, stolons, or creeping stems).

Table S2. The effect of fruit set between all five treatments. The five models were constructed using generalized linear mixed models with binomial errors. We used the relevel function to test the effect between all treatments.

Treatments	**Pollen added**	**Autonomous**	**Self**	**Cross**
Natural	$z = -4.30$; $P < 0.05$	$z = -1.93$; $P = 0.05$	$z = -5.51$; $P < 0.05$	$z = -5.59$; $P < 0.05$
Pollen added		$z = 2.48$; $P = 0.01$	$z = -1.31$; $P = 0.19$	$z = -1.41$; $P = 0.16$
Autonomous			$z = -3.76$; $P < 0.05$	$z = -3.84$; $P < 0.05$
Self				$z = -0.10$; $P = 0.91$

Chapter 5: Thesis Conclusions

This thesis comprises three studies that set out to gain a better understanding of plant invasions, using Proteaceae as a test case. Each study assessed determinants of invasions at different stages along the introduction-naturalization-invasion continuum. Specifically, I wanted to understand the patterns and processes that are important for species invasiveness and habitat invasibility.

Current impacts by plant invaders highlight the importance of identifying which species have the potential to successfully invade once introduced into a novel range. Two approaches are commonly used: a species approach (i.e. invasiveness) and a community approach (i.e. invasibility) (Richardson and Pyšek 2006). On the one hand, there are particular traits associated with invasiveness that are common among invasive alien plants (Goodwin *et al.* 1999; Hamilton *et al.* 2005; Pyšek and Richardson 2007b). On the other hand, there are common characteristics of the recipient environment which typically drive invasions (Colautti *et al.* 2004; Lozon and MacIsaac 1997; Thuiller *et al.* 2005). These approaches have mostly been studied independently. However, invasions are complex, and combining these approaches is necessary to derive insights that explain biological invasions and which are useful for management.

Horticulture is a pathway that has been associated with many invasive plants (Dehnen-Schmutz and Touza 2008). Proteaceae has recently become favoured in horticulture. Unlike *Pinus* and Australian *Acacia* species which are mainly planted around the world for forestry purposes, Proteaceae are largely introduced for horticulture. Given that relatively few species have become invasive in this group (2% of introduced species), assessing determinants of plant invasions is necessary to identify potentially invasive species amongst recently introduced species. The introduction of many Proteaceae species to many localities provides useful opportunities to draw important insights on drivers of biological invasions.

Here we show that, invasive alien plants possess several traits which allow them to become invasive in the introduced range. Introduced Proteaceae species with large native ranges, those planted as a hedge or barrier plants, are tall in stature, produce small seeds that are stored in woody follicles which are released after fire are most invasive. Clearly, these traits confer invasiveness in this group (chapter 2). In addition, reproductive traits are also important for invasiveness (Richardson *et al.* 2000b). Self-compatibility, generalized pollination requirements and the presence of pollinators in the introduced range are likely to maintain seed production (shown for *Hakea salicifolia*) and in some cases increase seed production (shown for *Banksia* species). However, reproductive barriers do not limit the spread of Proteaceae species in South Africa (chapter 4). By looking at species at different stages of the invasion continuum we identified factors that contribute to successful invasions: high propagule pressure, suitable climatic conditions, and disturbed (i.e. natural and human-mediated) habitats (chapter 3).

Traits identified as being associated with invasiveness in this study have also been shown to be important in other studies. For example, large native range size is correlated with invasion success for Australian *Acacia* species (Hui *et al.* 2011) and several introduced seed plants that are native to Central Europe (Pyšek *et al.* 2009; Shah *et al.* 2012), hence there are a few general attributes of plant invasions. Single traits provide little predictive power, but several traits in combination define syndromes that may explain invasion success (Levine *et al.* 2003) and which are useful for predicting further invasions.

In chapter 2, I assessed a set of traits that could potentially explain which factors are important for naturalization and invasion at a global scale. I found that some variables show similar selection for naturalization and invasion (e.g. large native ranges). Other variables are only important at one stage (e.g. taller species become invasive), and some show selection in differing directions as invasion progresses (e.g. large seeded species are more likely to naturalize but small seed size is strongly associated with invasion success).

In chapter 3, I explored which mechanisms underlie naturalization by examining the status of Proteaceae species introduced into South Africa. I focused on species that are not already classified as major invaders. This study confirmed that, on a regional scale, habitat invasibility is primarily determined by propagule pressure of *Hakea salicifolia* in areas where climatic conditions are suitable. However, several human-mediated factors potentially play a role in areas with suboptimal climates. Moreover, disturbance regimes facilitate naturalization of *Banksia* species in South Africa.

In chapter 4, I assessed the breeding systems of five *Banksia* species and *H. salicifolia* in order to understand whether pollination drives invasions on a local scale. This study confirmed that fruit production of the species studied in South Africa is not limited by pollinators and autonomous self-fertilization since all studied species are visited by an array of pollinators and are self-compatible. There is therefore no evidence that reproductive performance is a fundamental barrier to invasion.

Overall, I found that different traits become important at different spatial scales and at different stages in the invasion continuum. For some species, the importance of traits is consistent across the different dimensions (i.e. scale and stage) but vary in other species. This is supported by other studies which also consider spatial scale or stage of invasion (Milbau and Stout 2008; Theoharides and Dukes 2007; van Kleunen *et al.* 2010; Williamson 2006). For example, I found that on a global scale large native range size is positively associated with the likelihood of species surviving and naturalizing in new ranges. Once these species are introduced, this characteristic is also associated with species that become invasive on a regional scale. In contrast, the susceptibility to the root-rot fungus *Phytophthora* limits survival and naturalization in the new range, but only resistant species can progress and become invasive. This information can be used to improve the management of invasive alien plants and identify potentially invasive species. Furthermore, these results demonstrate the importance of assessing, in combination, the many facets (i.e. spatial scale, invasion stage, pathways, species traits and characteristics of the recipient environment) that are known to drive biological invasions.

This study demonstrates that compiling trait databases, conducting population surveys in the recipient environment, and performing field experiments on species traits are useful for understanding invasion dynamics. Furthermore, future studies should consider (in combination):

1. Research focused on particular taxonomic groups
2. Identify species traits as well as characteristics of the recipient habitat that drive invasions
3. Conduct comparative studies of species that are placed at different stages in the introduction-naturalization-invasion continuum
4. More importantly, studies should also consider traits of non-introduced species. This was a major limitation in this study.

To achieve the goal of predicting successful invasions, the recommendations mentioned above must be jointly accounted for in order to increase our predictive power. I recommend future studies to use a similar framework for other plant groups. These types of studies will provide a better understanding of why some introduced species become invasive while others fail and will ultimately assist in managing biological invasions. The work presented in this thesis contributes to understanding the causes and mechanisms of plant invasions and address questions of species invasiveness and community invasibility.

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