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Tanya J. Mason
University of Wollongong

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**Impacts of plant invaders and management
techniques on native communities: ecological and
social perspectives at regional and global levels**

A thesis submitted in fulfilment of the requirements for the award of the degree of

Doctorate of Philosophy

from the

University of Wollongong

by

Tanya J. Mason B. Sc. (Hons)

School of Biological Sciences

2006

Thesis Certification

I, Tanya J. Mason, declare that this thesis, submitted in fulfilment of the requirements for the award of Doctor of Philosophy, in the School of Biological Sciences, University of Wollongong, is wholly my own work unless otherwise referenced or acknowledged. The document has not been submitted for qualifications at any other academic institution.

Tanya Mason

November 2006

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Abstract

Plant invasions of natural communities threaten biodiversity and ecosystem processes across many biomes and trophic levels. Understanding and managing invader impacts are therefore significant steps in achieving conservation. Both causes and management of invasion are dependent on human behaviour and ecologists must consider this human dimension in developing management protocols. While control of invaders is routine in many conservation reserves, assessment of ecological outcomes following control is rarely enacted. Management is itself a disturbance and the compounding effects of both invasion and management on biodiversity merit rigorous assessment. While species-level responses to plant invasion have been widely reported, functional group and seed bank responses to invasion and management are rarely investigated. Generalisations about invader impacts are urgently required for targeted restoration. In this thesis, I used qualitative review, field study and meta-analysis to address ecological, social and land management issues of invasion biology.

Firstly, I reviewed policy instruments and asked: are government, land managers and the scientific community using available social levers to achieve optimal invader management? I found that while important policy principles have been developed, they require greater enactment. Release of significant funds will be required to resource long-term invader control and restoration activities. Education and voluntary incentives require a strong extension service to maintain involvement and standards of control. Rigorous monitoring systems are an under-utilised but important tool in achieving adaptive invader management.

I then used the invasive shrub bitou bush, *Chrysanthemoides monilifera* ssp. *rotundata*, to analyse invasion and management impacts in coastal dune communities of

eastern Australia. I compared the effects of intensive, manually-based invader control with those of extensive control (mainly herbicide spraying from aircraft) across fore dune communities. I examined one management regime, which was typically intensive, in hind dune communities. My main aim was to test the prediction that intensive methods would achieve better biodiversity outcomes than extensive approaches in fore dune communities. I found that extensive management created native species complements that diverged from non-invaded sites while intensive management approached non-invaded site conditions. However, intensively managed sites were also richer in other exotic species than extensively managed sites. Thus, while biodiversity outcomes were better under intensive management, the risk profile of such sites was increased by the greater array of exotics that could potentially replace the original invader. The positive effects of management evident on some fore dunes were not found in hind dunes, where managed sites had the highest exotic species richness and similar bitou bush seedling abundance as both non-invaded and bitou-invaded sites. Hind dune managed sites were also compositionally distinct from non-invaded sites. For all sites, even after intensive management, follow up control is required to avoid substitution of the primary invader by other aggressive invaders.

In order to characterise invader impacts beyond species-level comparisons, I compared bitou bush impacts on vegetation structure, richness of both native and exotic growth forms and community variability in fore and hind dunes. I found that bitou bush impacts were context specific: in fore dune shrublands, functionally distinct graminoid, herb and climber rather than shrub growth forms had significantly reduced species richness following bitou bush invasion. However, in forested hind dunes, the functionally similar native shrub growth form had significantly reduced species richness following bitou invasion. Density of vegetation structure increased at the shrub level in

both fore and hind dune bitou-invaded, relative to non-invaded communities. Fore dune ground-level vegetation density declined at bitou-invaded sites compared with non-invaded sites reflecting significant reductions in herb and graminoid species richness. Hind dune canopy-level vegetation density was reduced at bitou-invaded compared with non-invaded sites. Bitou bush invasion also affected fore dune community variability with significant increases in variability of species abundances observed in bitou-invaded compared with non-invaded sites. In contrast, there was similar variability among all hind dune sites. The results suggest that effects of bitou bush invasion are mediated by the vegetation community.

In addition to standing vegetation dynamics, I investigated soil-stored seed banks affected by bitou bush invasion and management, to further elucidate levels of community resilience. While management of bitou bush may have reduced the density of bitou bush seeds in the soil, it did not reduce the richness of other exotic species. Native tree seed richness was significantly higher in seed banks of sparsely-invaded than either heavily-invaded or managed hind dune sites, perhaps indicating a permanent shift in community structure following invasion. However, remaining indices of native seed bank diversity were similar across all invasion categories, indicating that seed banks of many native species were unaffected by both invasion and management. While examination of seed banks is informative in assessing past and potential community dynamics, low similarity between the standing vegetation and seed bank at all sites indicated that many hind dune species had other storage or regeneration modes and seed banks cannot be relied upon for comprehensive dune restoration.

Finally, I used meta-analysis to contextualise my field studies of bitou bush invasion using 20 international invasion studies. I hypothesised that plant invaders act as biotic filters and more strongly affect representation of some plant traits over others

in the resident community. I analysed the effects of graminoid and woody invaders on species richness for native growth form, longevity, seed mass and flowering phenology traits. I found that graminoid invaders disproportionately affected species with graminoid and herbaceous growth forms, perennial strategies and small seed masses. Woody invaders disproportionately affected graminoid or shrub species and perennials. Woody invaders had a consistently greater negative effect on native species than graminoid invaders, perhaps due to pre-emption of light resources. In contrast, it made no difference to native richness as to whether species flowered at the same time as the invader, indicating little interaction between invader and native pollination dynamics.

Plant invaders non-randomly affect resident species in turn changing community attributes. Current management of invaders may not re-instate pre-invasion conditions. Restoration is dependent on recognising the impacts of an invader and both supplementing native traits adversely affected by invasion and enacting long-term follow-up control of primary and secondary invaders.

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Chapter 1

General Introduction

Preface

My thesis addresses the effects of plant invaders on native communities, the social framework for invader control and the ecological success of on-ground control techniques following invasion. Firstly, I discuss social levers important for management of invaders in Australia. I use bitou bush *Chrysanthemoides monilifera* ssp. *rotundata* to investigate specific invader effects and control activities. I then contextualise these findings by investigating general impacts of graminoid and woody invaders across a number of biotas. In this general introduction, I define and describe the process of plant invasion, summarise the known impacts of invasion and discuss the options for invader management. The introduction also provides background information about bitou bush: its status, distribution, invasion history, impacts in native dune communities and control techniques. The thesis chapters have been written as journal articles. This thesis style necessitates some repetition of introductory and methodological information to allow autonomy of each chapter. The introductory section of each chapter provides detailed reference to pertinent literature and theoretical concepts, thus allowing this general introduction to function as an overview.

What is a plant invader?

Richardson et al. (2000a) defined invasive species as plants which naturalise or independently establish and produce reproductive progeny at considerable distance from parent plants. Invasive plants overcome geographic, environmental, reproductive and dispersal barriers and occur in both disturbed and undisturbed natural habitats (Richardson et al. 2000a). I use the terms ‘weed’, ‘invader’ or ‘exotic’ interchangeably

to describe species which are invasive in natural vegetation. Invaders adversely impact native biodiversity values and may also change ecosystem function.

Ecologists have repeatedly attempted to predict invader attributes to inform pre-importation risk assessments. Baker (1965) identified a number of important invader traits including self-compatibility, seed longevity, rapid seedling growth, vigorous vegetative growth and competitive morphology such as a smothering growth form. Further attributes of potential invaders may include efficient dispersal (often via human vectors) flexible life history or use of resources, high population growth rate, short life cycle and high resource allocation to reproduction (Bazzaz 1986, Orians 1986). Many of these attributes are displayed by ruderal, agricultural or horticultural weeds. However, invaders have a wide variety of demographic traits and ecological roles and include ferns, gymnosperms, aquatics, vines, shrubs, trees, annuals, biennials and perennials (Randall 1997). Invader traits are therefore difficult to predict. In many cases, taxonomic composition of invader species is non-random (Crawley 1987) and reflects factors such as human migration and agricultural or ornamental utility. However, invasion success may also depend on attributes of the invaded community. Frequency and intensity of human-mediated disturbance, indigenous species richness, distance to potential immigrants and similarity between source and invaded habitats influence invasion success (Crawley 1987).

Consequently, the predictive capacity of trait information in determining invasibility remains low (Radford and Cousens 2000, Byers et al. 2002). Attributes of both the invader and the invaded community interact in defining invasion status thus complicating predictability. Furthermore, species compositions, disturbance, climatic variables and resource availability (Crawley 1987, Byers et al. 2002) reduce the predictive power of invasion ecology. The lack of predictability suggests that, rather

than aiming to predict invasion events, strengthening of quarantine at multiple scales and eradication, control or management of existing invaders may prove more profitable (Smith, CS et al. 1999).

Invasion ecology: development of a mechanistic approach

Biological invasion occurs when an organism extends its previous range (Vermeij 1996, Williamson 1996). It may be a natural phenomenon facilitated by climate change, continental drift, migration via air and ocean currents, and evolution. However, human-mediated introductions, both deliberate and accidental, have accelerated the invasion process by overcoming biogeographical barriers to dispersal (Tilman and Lehman 2001). The invasion process involves arrival and establishment, spread and finally equilibration (Williamson 1996) of an organism in a novel environment. As increasing taxa complete the invasion process, homogenisation of flora across communities becomes evident (McKinney 2004).

Important invasion ecology concepts have incrementally developed over the past 150 years. Darwin made many observations fundamental to invasion ecology in his seminal work *On the Origin of Species by Means of Natural Selection* (Darwin 1875, Rejmánek 1996, Lunsin and Wolfe 2001). However, Elton is generally recognised as establishing the research field with publication of *The Ecology of Invasions by Animals and Plants* (Elton 1958). Through his studies of native and exotic species on oceanic islands, Elton (1958) concluded that richer communities were less invisable. This concept of biotic resistance was reinforced by the dynamic equilibrium model of island biogeography (MacArthur and Wilson 1967).

Subsequent experimental studies supported a negative relationship between native and exotic species richness (Knops et al. 1999, Levine 2000, Naeem et al. 2000, Kennedy et al. 2002) which has been explained by competitive processes (Huston

1999). However, meta-analysis of competition studies revealed that ‘biotic containment’ rather than ‘biotic resistance’ may be a more appropriate term when assessing invader establishment and performance: native species interactions may regulate invader abundance rather than completely repel invaders (Levine et al. 2004). In contrast, observational studies have reported a positive relationship between native and exotic species richness (Stohlgren et al. 1999, Sax 2002a, Cully et al. 2003). This apparent paradox may be resolved through consideration of spatial scale in invasion studies. Shea and Chesson (2002) proposed that where extrinsic factors remained constant in small scale experimental studies, a negative relationship between numbers of native and exotic species existed, due to higher native richness resulting in fewer niche opportunities for invaders. However, as scale increased, extrinsic factors (such as latitude, climate and soil type) varied resulting in increased niche opportunities for invaders and leading to an overall positive relationship between means of native and exotic richness values. Davies et al. (2005) argued that the mechanism explaining positive correlations between native and exotic richness related to heterogeneity in species composition (beta diversity) and abiotic conditions rather than mean abiotic conditions alone.

A number of processes have additive or synergistic effects on the establishment and growth of an invader. I summarise interacting processes which contribute to invader success in Figure 1.1. I then discuss each component in turn.

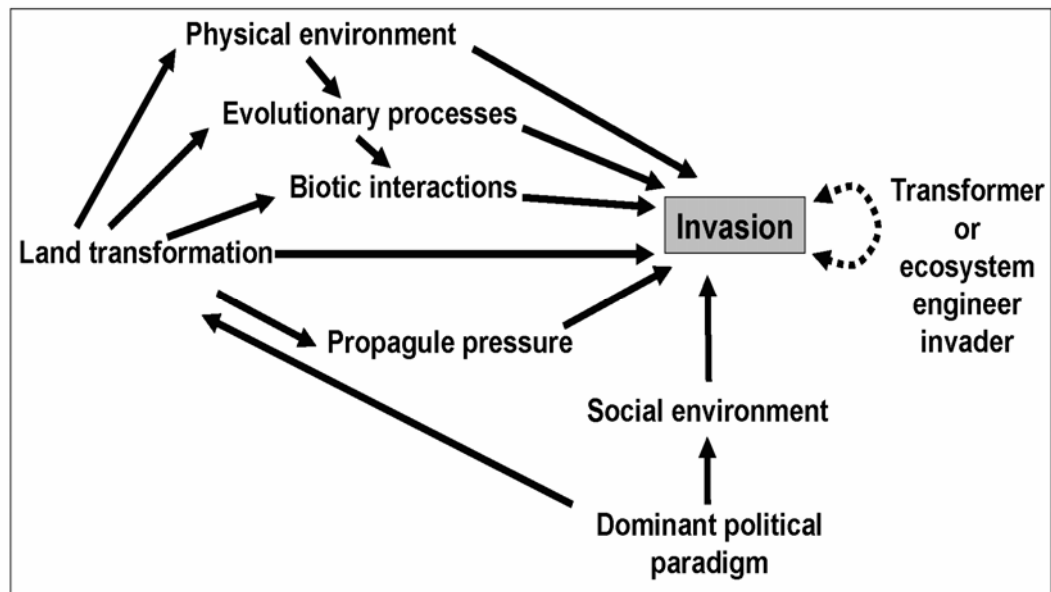


Figure 1.1: Generalised processes contributing to the success of an invader in a novel community. Feed back may occur between many of the illustrated processes.

Land transformation

Prior to human settlement, interactions of climatic, edaphic and landform factors primarily determined the level of ecological heterogeneity in the landscape (Groves and Hobbs 1992). Human colonisation, particularly in modern times, has irrevocably altered the landscape. Cropping, grazing, forestry clearing and utility construction have removed indigenous vegetation and altered physical profiles. Clearing has also facilitated urban land uses. Such activities have progressively simplified and fragmented original landscape patterns. Land transformation is a direct determinant of invader success because dispersal foci for invaders are often associated with human-modified systems (Vitousek et al. 1997a) such as ornamental and agricultural land uses. As invaders spread and dominate natural systems they feed back and transform the natural landscape further (D'Antonio and Vitousek 1992).

Land transformation may also indirectly affect invader success. Fragmentation and isolation of previously contiguous natural ecosystems change pollination and

dispersal dynamics (Cunningham 2000, Kolb and Diekmann 2005). Reducing the size and increasing the isolation of native plant populations may reduce their viability through stochastic events, inbreeding depression and allee effects on reproductive success (van Groenendael et al. 1998, Lennartsson 2002, Oostermeijer et al. 2003). While these fragmentation processes operate on native and invader species alike, invader species may be pre-adapted to fragmentation, but native community resistance may be compromised following reduced community diversity, in turn enhancing the probability of successful plant invasion (e.g. De Grandpré and Bergeron 1997).

Propagule pressure

Propagule pressure, composed of seed rain and aerial or soil-stored seed banks, reflects surrounding land uses, landscape processes, pollination dynamics, dispersal vectors and predation rates. Native propagule pressure may be reduced by landscape transformation. For example, fragmentation may affect the identity and effectiveness of seed dispersers (Santos et al. 1999) and pollinators (Kolb 2005) and may increase local extinction risks of plants with a low self-pollination capacity (Lennartsson 2002). Further, many native species, particularly early successional species, are seed limited – as demonstrated by seed augmentation studies (Turnbull et al. 2000). Consequently, autecology and land transformation may compound and decrease native propagule pressure.

In contrast to declining native propagule pressure, invaders with increased representation in the human-modified matrix, have high propagule pressure and increasingly contribute to the seed rain and soil seed bank of native communities (Tucker and Murphy 1997). Indeed, propagule pressure has been recognised as important in determining the invasibility of a region (Williamson 1996, Lonsdale 1999). Increasingly, studies have attributed invader dominance to greater propagule dispersal

of invader over native species rather than the oft cited mechanism of superior competitive abilities (Seabloom et al. 2003a, b, MacDougall and Turkington 2005).

Evolutionary processes

Plant invasion of native communities may have important evolutionary consequences for natural systems. Although evolutionary changes are often not detectable in ecological time (Williamson 1996), organisms do exhibit a dynamic evolutionary relationship with the environmental stresses they encounter (Sousa 1984). Successful invaders are generally pre-adapted to the environments in which they invade. However, factors such as genetic drift and natural selection may also act to accelerate adaptive evolution of the invader in novel environments (Sakai et al. 2001), while hybridisation between species or between distinct source populations may enhance invasiveness (Ellstrand and Schierenbeck 2000).

Further, evolutionary processes may interact with the physical environment to change selective pressures and enhance invasion. Native species which have adapted to prevailing conditions may be competitively inferior under novel, human-mediated disturbance. Invading species may out compete native species before they evolve to the new optimum (Byers 2002). Evolutionary processes are also linked with propagule pressure. High propagule immigration facilitates gene flow and may provide sufficient genetic variation in the population to allow adaptive evolution of the invader (Sakai et al. 2001).

Physical environment

Abiotic factors such as temperature extremes, water and light availability, soil composition and exposure interact to characterise the physical environment. These abiotic factors, coupled with plant physiology and morphology, determine species distributions. Alterations to the physical environment may represent an endogenous

disturbance which occurs naturally and periodically in a vegetation community (e.g. wildfire or flooding). Alternatively, the disturbance may be exogenous to the system and may either change an endogenous disturbance (e.g. increase fire frequencies) or represent a novel event (e.g. nutrient addition) (Fox and Fox 1986). Exogenous disturbances are a feature of human-modified landscapes. Activities such as grazing, mining, recreation and fertilisation change availability of resources in the physical environment and ultimately change plant distributions.

An increase in resource availability (such as light or moisture), either through resource release by residents or increased supply, creates an invasion opportunity (Davis et al. 2000). Importantly, resource availability may change through time such that site invasibility is not fixed (Davis et al. 2000). A number of studies have documented increased invasion following changes to resource availability. Hobbs and Mooney (1991) investigated rainfall variability and soil disturbance in serpentine grasslands and found *Bromus mollis* invasion required both soil disturbance and high rainfall. Davis et al. (1999) simulated extended wet and dry periods under different nutrient regimes and found increased woody seedling survival in herbaceous vegetation with increased moisture but decreased survival with nitrogen addition. A review by Dukes and Mooney (1999) speculated that global change through increased atmospheric carbon dioxide concentrations, climate change and increased nitrogen deposition may increase the incidence of plant invasions. However, a study by Walker et al (2005) of *Hieracium pilosella* invasion of tussock grasslands did not support the concept that fluctuating resource availability facilitates invasion. Walker et al. (2005) found that invasion success did not differ under periodic or continuous disturbance regimes in a long-term experiment. Such a study cautions against generalisations that resource pulses create long-term invasion opportunities.

Biotic interactions

Biotic interactions such as competition, herbivory and mutualism contribute to plant community composition and diversity and are therefore integral to invader success. Competition has often been identified as a mechanism of invader dominance with invaders strongly limiting growth, reproduction and resource allocation of residents (Levine et al. 2003 and references therein). Direct competitive abilities are determined by factors such as an individual's maximal height, maximal photosynthetic and respiration rates and nutrient requirements (Tilman 1988). Direct competitive superiority has been established for a number of invaders (e.g. Owens 1996, Morris et al. 2002). Invaders may also attain a competitive advantage indirectly through escape from specialist and generalist herbivores, pathogens or diseases present in their native range. When a species is introduced to a region, the enemy release hypothesis predicts that specialist enemies from that species native range will be absent, host switching by resident specialists will be uncommon and generalists will impact native competitors more than the introduced species (Crawley 1987, Keane and Crawley 2002). Thus the introduced species suffers less damage from enemies than native competitors and dominates through competitive release.

Studies have reported increased reproductive effort and biomass production of species in their exotic range compared with their native range (Noble 1989, but see Thebaud and Simberloff 2001). However, there are little data on the impact of enemies, making it difficult to attribute these observations to enemy release: alternative hypotheses of inherent invader competitive advantage or favourable response to disturbance by the invader relative to natives remain viable (Keane and Crawley 2002).

Recently Blumenthal (2005), hypothesised that resource availability and enemy release may interact to enhance invader success in novel environments. Fast growing, high resource plant species often show high susceptibility to enemies because their

growth strategy invests little in enemy defence and results in high palatability. If such species invade novel environments, they are likely to exhibit a compounding positive response to both resource availability and natural enemy release, thus increasing the probability of invasion success.

Mutualism may also be an important process in determining invader success. Invasion may be aided by mutualisms such as animal-mediated pollination and seed dispersal, along with mycorrhizal associations (Richardson et al. 2000b). Plant species with highly specialised mutualisms are less likely to establish and spread in introduced ranges than invaders with general mutualisms (Richardson et al. 2000b). For example, Terwilliger and Pastor (1999) found that conifer invasion into meadows was limited by the absence of ectomycorrhizal fungi. Further, Rudgers et al. (2005) found that *Lolium arundinaceum* was better able to invade high diversity communities when in association with an endophytic fungus than when the mutualism was absent.

Social environment

While factors such as resource availability, physical conditions and biotic interactions are recognised as contributing to invader success (Shea and Chesson 2002), the influence of the social environment is rarely evaluated in invader studies. Social levers such as regulation, voluntary incentives, education and economic instruments determine the level of control effort. Invader control programs then manipulate the density of an invader at different life stages and ultimately influence the extent and impact of the invader in a community.

The social environment also influences numerous other landscape and ecological processes which interact to indirectly affect invasion status. Anthropogenic disturbance may cancel the selective advantage of native species which adapted *in situ* to environmental conditions, and create novel conditions which may favour invaders

(Byers 2002). Social policy dictates the rate and extent of anthropogenic disturbance such as land clearing, grazing and mining. Policy also determines the level of protection afforded to biotic interactions. For example the *Threatened Species Conservation Act (1995)* in New South Wales (NSW) has provisions for bitou bush control in order to abate threats to a number of native vulnerable or endangered species where bitou bush is invasive.

Transformer species

A subset of invaders is able to transform or engineer their environment once they establish and their effects feed back into the system. Transformers may excessively sequester resources such as water or light, provide previously limiting resources such as nutrients, suppress or promote disturbance or accumulate resources such as litter or salt which, in turn, limit plant growth (Richardson et al. 2000a). Documented examples of transformers include grass invaders such as *Agropyron desertorum* and *Andropogon gayanus* which may sequester water resources and change fire regimes: the fine fuel of grass invaders may increase fire frequency, extent and intensity (D'Antonio and Vitousek 1992, Rossiter et al. 2003). Leaf litter from the herb *Mesembryanthemum crystallinum* releases accumulated salt into the soil and reduces growth of native grassland species (Vivrette and Muller 1977). The nitrogen fixer, *Myrica faya*, increases nitrogen availability in a nitrogen-limited Hawaiian forest community (Vitousek 1990). Since Vitousek's seminal study, impacts of a number of other nitrogen fixers have been reported. For example, *Acacia saligna* in South African fynbos (Yelenik et al. 2004) and *Falcataria moluccana* in Hawaiian forests (Hughes and Denslow 2005) elevate soil nitrogen and alter species compositions.

Transformers may also release novel allelopathic chemicals into the soil which may competitively advantage the transformer by modifying neighbour nutrient

acquisition or altering the soil biota (Callaway and Ridenour 2004). Species which release allelopathic chemicals have been observed to adversely impact neighbouring species in novel environments (Steenhagen and Zimdahl 1979, Callaway and Aschehoug 2000). Consequently, allelopathy may be an important biochemical mechanism utilised by invaders to competitively dominate native communities. By altering the chemical environment, allelopathic invaders may also act as ecosystem transformers and change species compositions.

Impacts of invaders

While the mechanism of invasion may depend on attributes of the invader, the impacts of invasion on the native community are frequently similar across invader types. Commonly, invasion results in reduced native species richness. Species may strongly interact with the invader and suffer competitive exclusion, or may weakly interact with the invader and lose representation due to seed limitation or sensitivity to novel disturbance (Seabloom et al. 2003a, b, MacDougall and Turkington 2005). In both cases, resident communities suffer species loss. This process is frequently non-random (Grime 1987, Giller et al. 2004) and results in reduced biodiversity value of the invaded community.

Invaders have selectively affected particular plant traits in resident communities in a number of studies. For example, the invasive climber cape ivy, *Delairea odorata*, disproportionately affected forb and to a lesser extent graminoid growth forms over other growth forms in scrub and riparian vegetation of coastal California. The authors hypothesised that forb and graminoid growth forms were particularly negatively affected by invasion because they had significant overlap in resource use with the invader (Alvarez and Cushman 2002). Invasion of South African fynbos shrublands by the shrub *Acacia saligna*, changed guild structure (Holmes and Cowling 1997a). Long-

invaded fynbos had proportionately more vertebrate-dispersed species, and less short shrubs and shrubs with ericoid leaves than non-invaded fynbos. Further, recruitment of all growth forms except for forbs and non-thicket resprouters was proportionately less frequent in long-invaded than non-invaded fynbos (Holmes and Cowling 1997a).

Christian and Wilson (1999) recorded exclusion of growth forms similar to the invader following invasion of prairie sites by the graminoid *Agropyron cristatum*. Native tree recruitment may also decline following woody invasion (Woods 1993). In contrast, Yurkonis et al. (2005) found that examples of climber, shrub, grass and herb invaders in abandoned agricultural fields lacked strong growth form interactions with residents: invaders did not disproportionately affect growth forms similar to themselves in the resident community.

While some studies have revealed striking examples of the selectivity of invader impacts on plant traits or reproductive strategies, most invader studies examine impacts based on overall species richness values alone. However, species richness is an incomplete measure of biodiversity (Wilsey et al. 2005) and predictor of ecosystem processes (Downing 2005). Consequently, in this thesis, I investigated a number of other diversity measures in quantifying invader impacts. I addressed site-to site variability following invasion: changes to species richness and composition may affect stability of ecosystem properties (Hooper et al. 2005). I also addressed ecological redundancy. Redundancy occurs when a number of species perform equivalent functional roles yet are differentiated along an environmental gradient. Loss of one species may be compensated by other species in the functional group. This compensatory response maintains ecosystem function. Redundant species therefore improve ecosystem resilience to perturbations (Walker 1992, 1995). In the extreme case, invasion may result in the loss of an entire functional group or plant trait.

Conversely, the invader may represent a novel functional group – in both cases the invader may cause dramatic changes to ecosystem function. Invasion ecology must search for generalisations about the impact of different types of plant invaders on native communities. Such research may inform restoration efforts without the need for site assessment. Results of individual invader impacts are increasingly reported and require synthesis. Meta-analysis is a useful tool in statistically synthesising individual case studies and may assist prioritisation of control effort (Byers et al. 2002).

A related issue is that strikingly few studies have compared the effects of a single invader in multiple habitats (Alvarez and Cushman 2002). Numerous major invaders are capable of affecting a diversity of habitats. For example, *Lantana camara* may invade both dry rainforest and savanna woodland (Fensham et al. 1994) while *Pinus nigra* may invade both fore dune and forest edge communities (Leege and Murphy 2001). In many cases it is unclear whether effects of a single invader are consistent across habitats and it is important to establish the status of an invader in multiple habitats to determine management priorities at a landscape level.

Transformer invaders may directly affect delivery of ecosystem services by affecting nutrient cycling, fire regimes and hydrology (Levine et al. 2003 and references therein). Such invaders are exemplified in Section 1.2.7 above. The impacts of transformers on ecosystem services of direct benefit to human populations has been highlighted by the South African *Working for Water* program which has quantified impacts of tree and shrub invaders on water delivery. The invasion process has increased plant biomass and reduced runoff which may ultimately affect human water supplies. In addition, the invaders have increased fire intensity and promoted soil erosion (Le Maitre et al. 1996, van Wilgen et al. 1996, van Wilgen et al. 1998).

Transformer invaders modify the biotic or physical environment and may catalyse an

invasional meltdown (Simberloff and Von Holle 1999) where the primary invader facilitates invasion by secondary species. While transformer invaders may affect delivery of ecosystem services for human populations, many invaders of natural systems require considerable control effort regardless of their transformer status. Such control operations demand financial support and incur ongoing social costs: monies expended on invader control cannot be applied to projects such as conservation reserve expansion or other common good projects of health and education.

Species loss through invasion may change the quality or quantity of interactions between species at different trophic levels and ultimately change community structure (Hoffmeister et al. 2005). Plant invader impacts on fauna are rarely reported (French and Major 2001), but invader-induced changes to plant structure are likely to affect the quality of fauna habitat. For example, one study reported increased nest predation of songbirds utilising invader over native shrub species. Invader species had sturdy, thornless branches and reduced basal cover which afforded less protection from predators than native species and therefore exposed nests to higher predation (Schmidt and Whelan 1999). Plant invaders may also change soil fauna diversity and food-web structure (Kourtev et al. 1999, Belnap and Phillips 2001). For example, a study by Ernst and Cappuccino (2005) found that a number of arthropod-feeding guilds (gall-makers, gall miners and pollen/nectar feeders) were absent or poorly represented on individuals of an exotic vine *Vincetoxicum rossicum* which invades old-field communities in Canada. Changes to invertebrate diversity may ultimately affect decomposition and nutrient mineralisation rates (Parker et al. 1984) in invaded ecosystems.

Overwhelmingly, the invasion literature has reported negative impacts of plant-invaders. However, invaders may also have neutral or positive impacts on some biodiversity measures. For example, Sax (2002b) found species richness remained

similar despite turnover in species composition for many trophic levels in native and invaded Californian woodlands. Additionally, the exotic shrub *Rosa rubiginosa* reportedly functions as a nursery plant in Argentinean sub Antarctic forests by providing a favourable microclimate for establishment of native species in areas degraded by grazing activities (de Pietri 1992). Invaders may also provide forage or cover for native fauna (reviewed in D'Antonio and Meyerson 2002). Importantly, invaders are valued in anthropogenic or disturbed native systems where they provide a suite of services previously supplied by native species (Williams 1997). However, as disturbed systems are restored, beneficial attributes of invaders diminish and they may be actively removed in the goal of ecosystem restoration.

Management of invasion

A number of control techniques have been developed to reduce or eradicate invader biomass and restore native community dynamics. These techniques may vary in specificity, labour intensity and on-ground disturbance (Table 1.1). Targeted, labour intensive control techniques are applied over small areas and have the advantage of targeting the invader while minimising damage to native species. However, these techniques involve on-ground action which may result in significant localised soil disturbance (Ussery and Krannitz 1998) and require considerable financial resources to meet labour demands. In contrast, non-targeted control techniques are used to reduce invader biomass over large areas and where access is difficult. Non-targeted control techniques allow extensive control of invader propagule pressure and remote application reduces localised disturbance to native communities. Further, costs of application are reduced when compared with labour-intensive approaches (Serbesoff-King 2003). For example, Paynter and Flanagan (2004) estimated control costs of AUD\$50 ha⁻¹ to control *Mimosa pigra* via land-extensive control techniques of aerial herbicide

application followed by fire. In contrast, control costs of *Rhododendron ponticum* in Britain using labour intensive techniques of combined manual and chemical removal was estimated at AUD\$972 ha⁻¹ (Dehnen-Schmutz et al. 2004). However non-targeted control may damage both the invader and native species in turn compromising post-control community recovery. For example, off-target drift from aerial herbicide programs may further threaten endangered species populations (Mataarczyk et al. 2002).

Table 1.1: Techniques to control plant invaders of conservation areas (adapted from Muylt 2001).

Control technique	Description	On-ground disturbance
Targeted and labour intensive	<ul style="list-style-type: none"> • manual removal of foliage, roots, tubers etc. and seedlings • cut, drill-fill, frilling, ring barking treatment of cut branches or boles, generally followed by application of herbicide to cut area • back-pack herbicide application to foliage 	high
Non-targeted and land-extensive	<ul style="list-style-type: none"> • aerial herbicide application to foliage • fire • slashing / mowing • mulching 	medium to low
Targeted and land-extensive	<ul style="list-style-type: none"> • biological control through release of insects or plant pathogens with high fidelity to the target invader 	low

Biological control offers the selectivity of labour intensive methods combined with low disturbance and control costs of land extensive methods (Fowler et al. 2000). However, the success of a biological control program may be variable (Denoth and Myers 2005). Often, the partial success of biological control necessitates implementation of integrated control where conventional chemical and mechanical techniques are combined with biological control to effectively suppress invaders (Fowler et al. 2000).

Long-term control of plant invasions requires follow-up and monitoring regimes regardless of the initial control technique. Invader populations may escape initial

control, resprout following treatment or germinate from the seed bank or seed rain and re-invade treated areas. Follow-up can target isolated invader populations which may otherwise form re-invasion foci (Moody and Mack 1988). Follow-up may also remove potential secondary invaders. In addition to follow-up works, plant invader management programs must include monitoring which tracks community dynamics along a restoration trajectory. In the past, monitoring was poorly implemented as a result of institutional inertia, funding discontinuities and prioritisation mechanisms within management agencies (Walters 1997, Simberloff et al. 2005). However, effective monitoring informs management decisions (Hobbs and Norton 1996, Yoccoz et al. 2001) by evaluating the biodiversity outcomes of control measures. Monitoring programs must follow a scientific design with adequate replication (often at multiple scales), inclusion of controls, assessment of detection probabilities and development of hypotheses (Yoccoz et al. 2001). Such monitoring is integral to adaptive management but is rarely consistently undertaken (Grice 2004).

Bitou bush Chrysanthemoides monilifera ssp. rotundata: an invader case study

Chrysanthemoides monilifera ssp. rotundata (DC) Norl., commonly known as bitou bush or bitou, is a sprawling to erect Asteraceae shrub. Bitou was presumably first introduced to Australia from South Africa as a ballast contaminant and established on the NSW north coast during the early twentieth century (Cooney et al. 1982). Following recognition of its sand-stabilising properties, it was actively planted to prevent coastal sand drift from 1946 to 1968 (Weiss et al. 1998). Deliberate planting ceased when the invasive character of bitou was recognised. However bitou continued to spread from source populations and the current distribution ranges from Pambula on the NSW south coast, north to Queensland with sporadic occurrences as far north as Rockhampton (Weiss et al. 1998). Bitou invasion is concentrated in NSW with over 70 000 ha of

vegetation invaded (CRCWMS 2001) and approximately 90% of the sandy coastline affected (Toth et al. 1996) (Figure 1.2). Bitou predominantly grows in sandy, infertile soils of coastal zones. It invades littoral communities such as dune grassland, shrubland, woodland and forest complexes along with rainforest and headland heath communities (Dodkin and Gilmore 1985). Bitou frequently achieves dominance in these communities and may form a dense shrub monoculture (T. Mason pers. obs.).

Figure 1.2: Distribution of *Chrysanthemoides monilifera* ssp. *rotundata* in New South Wales (DEC 2005).

A number of factors may explain the success of bitou invasion. Deliberate cultivation of the species may have allowed founder populations to increase beyond a threshold size in turn reducing the impact of environmental stochasticity (Mack 2000) and facilitating bitou establishment. Morphological features such as fleshy leaves and a vigorous, shallow root system may assist bitou to withstand salt and water stress in

coastal environments (Weiss et al. 1998). In addition, the phenology of bitou results in fruit production throughout the year, particularly during periods of little native productivity. Consequently, bitou seed is available for vertebrate dispersal throughout the year and periodically experiences little competition from native vegetation for dispersers (Gosper 2004) thus allowing efficient propagule transport. Indeed bitou seed banks have been recorded as ranging from 2 000 – 3 000 viable seeds m⁻² (Weiss 1984). Finally, rapid seedling growth and biomass production may provide a competitive advantage for bitou against native species (Weiss and Noble 1984a, b).

Bitou invasion has a number of documented impacts on native coastal systems. It displaces common native species such as *Acacia longifolia* ssp. *sophorae* (Weiss and Noble 1984a), *Banksia integrifolia* (Dodkin and Gilmore 1985) and *Correa alba* (Gray 1976). Furthermore, bitou threatens a number of endangered plant species and vegetation communities (*Threatened Species Conservation Act 1995 (NSW)*). Bitou invasion also alters abundance of leaf litter invertebrates and changes invertebrate compositions (French and Eardley 1997, Lindsay and French 2006). Finally ecosystem processes such as leaf litter decomposition and nutrient cycling are affected by bitou invasion: bitou decomposition is higher than native decomposition (Lindsay and French 2004) and soil nitrogen is higher in bitou-invaded areas than in non-invaded areas (Lindsay and French 2005). Consequently bitou may be a transformer invader. Additional nitrogen inputs by bitou in nutrient-poor coastal communities may alter ecosystem processes, ultimately promoting further bitou invasion directly through increased growth rates or indirectly through reduced performance of natives adapted to nutrient poor conditions (Lindsay and French 2005). While population- and ecosystem-level studies of bitou impacts have been undertaken, there is a dearth of plant community-level impact studies. Community interactions in non-invaded, invaded and

managed sites may broaden our understanding of bitou impacts and inform management decisions.

A number of control techniques are used to restrict distribution, density, reproduction and spread of bitou invasions. Targeted, labour-intensive techniques include hand pulling of small individuals and herbicide application to cut stumps or foliage. Foliage application of herbicide is achieved using back pack or vehicle-mounted spray units which allow the operator to target bitou individuals. Alternatively, non-targeted, land extensive control of bitou is achieved through aerial application of herbicide to dense infestations. Aerial herbicide application is non-targeted as native and bitou individuals alike receive herbicide spray. Glyphosate is the primary herbicide used in bitou control (Matarczyk et al. 2002), although other chemicals such as metsulfuron methyl have also been used (K. Hayes pers. comm.). In order to reduce native mortality during aerial operations, the herbicide is diluted and applied during winter when native susceptibility is low (Toth et al. 1993, Toth et al. 1996). However, the universality of low native susceptibility to herbicide has been questioned (Matarczyk et al. 2002) and long-term impacts of repeated herbicide application require evaluation.

Physical and chemical control of bitou may be integrated with other control techniques. Fire has been used to remove bitou biomass and stimulate native and bitou seed germination (Weiss et al. 1998, Vranjic et al. 2000a). In addition, a number of biological control agents have been released to reduce shoot, flower and fruit production (e.g. bitou tip moth *Comostolopsis germana*) and seed viability (e.g. seed fly *Mesoclanis polana*) (Holtkamp and Maguire 1993, CRCWMS 2001). Both fire and biological control techniques require integration with other strategies for effective regional control.

The range of on-ground bitou control programs has been facilitated by social instruments. The National Weed Strategy and NSW Weed Strategy articulate political awareness of detrimental invader impacts. Indeed, bitou is recognised as a weed of national significance by the federal government. In NSW, regulation through the *Noxious Weeds Act (1993)* and *Threatened Species Conservation Act (1995)* attempts to restrict the spread and density of bitou invasions. Economic instruments provide funding for on-ground bitou control operations. It has been estimated that labour, material and in kind contributions for bitou control cost approximately \$2 million per annum in NSW (CRCWMS 2001). Finally, voluntary community participation is vital in primary and follow up bitou control. Volunteer groups such as Coastcare provide long-term commitment to numerous coastal rehabilitation projects involving bitou removal and native species regeneration.

Despite considerable control effort directed at bitou invasion, monitoring programs which address the ecological success of control have been sporadic. Consequently, while the administrative parameters of bitou control are understood, the ecological outcomes of control are largely unknown. There is increasing recognition that weed control and restoration efforts may not reinstate pre-invasion communities but induce alternative persistent states (Suding et al. 2004). Studies are required to determine the extent and resistance of altered states following restoration effort such as weed control. These studies must address restoration potential through analysis both of standing vegetation and dormant community components such as soil-stored seed banks. Indeed, scientific designs may be applied to invader monitoring regimes: scientifically rigorous monitoring informs managers of progress towards ecological objectives and provides restoration ecology datasets to test relevant theory.

Project aims

This project aimed to aid our understanding of plant invader impacts in native communities and investigate social and ecological strategies available to control invaders. I initially investigated social perspectives in weed management in Australia, with specific reference to protocols in NSW. With an understanding of prevailing management tools, I aimed to determine the ecological success of the current structure. I used bitou as a case study invader because it is widespread in coastal dune communities of eastern Australia with documented impacts on native biodiversity (see section 1.3 above). Bitou is a high profile invader which has been a target of long-term control effort. I sought to quantify the ecological success of management techniques applied to bitou invasions and resolve the level of success against both management and the type of plant community. I focused both on standing vegetation and seed bank dynamics and addressed impacts both of the invader and management regimes. I then aimed to contextualise my findings from the bitou case study by conducting a meta-analysis of international invader impacts in natural systems.

The following research questions were addressed in this thesis:

1. Are government, land managers and the scientific community using available social levers to achieve optimal invader management?
2. How does bitou invasion and management affect species richness and composition?
3. Does bitou control reinstate native conditions, retain bitou-invaded conditions or impose a new plant community trajectory?
4. Does bitou invasion affect vegetation density and species richness among growth forms in fore and hind dune coastal communities?
5. Does bitou act differently depending on the resident vegetation community?
6. Does bitou invasion affect variability of dune communities?

7. Are hind dune soil-stored seed banks affected by bitou invasion and management?
8. Do woody and graminoid plant invaders, as biotic filters, consistently and similarly select particular growth form, longevity, seed mass or flowering phenology traits in the resident community and cause directional change in invaded community compositions?

Thesis format

Chapter 2 reviewed environmental weed control policy in Australia, focusing on the ability of government, land managers and the scientific community to utilise social levers to conserve natural areas and achieve weed eradication, control or management. Such levers include regulation, incentives, education, information, motivational instruments, property-right instruments and pricing mechanisms.

Chapter 3 specifically addressed the impact of bitou management regimes on dune communities of eastern Australia. In it I examined the efficacy of targeted, intensive, *versus* non-targeted, extensive bitou control in fore dune shrubland communities. I also examined management (typically intensive) regimes in hind dune woodland / forest communities.

Chapter 4 focused on the impact of bitou invasion in fore and hind dune communities. The impacts of invasion on species richness within growth forms, distribution of vegetation structure and community variability were examined.

Chapter 5 utilised a subset of NSW north coast hind dune sites to examine species richness and composition of soil-stored seed banks in (1) non-invaded, (2) managed and (3) invaded communities. Propagule pressure and seed bank richness are important considerations both for control and restoration initiatives.

Chapter 6 broadened the bitou-specific findings of earlier chapters and searched for generalisations in the invasion literature. I used meta-analysis to examine the effects of woody and graminoid invaders on resident communities across biomes. Invader impacts were quantified by comparing richness of resident vegetative and reproductive traits in both invaded and non-invaded communities.

Chapter 7 provided a general discussion with specific reference to implications of project findings for management and restoration activities.

Chapter 2

Environmental weed control policy in Australia: current approaches, policy limitations and future directions

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Introduction

Biological invasions are one of the most important drivers of biodiversity change (Lövei 1997, Vitousek et al. 1997b, Sala et al. 2000). Successful invasion of species to novel environments has numerous potential impacts, many well documented in the literature: invasion has resulted in reduced abundance of native species, species extinctions, alteration to ecosystem level processes and genetic and evolutionary change (Williamson 1996, Vitousek et al. 1997a). Traditionally, ecologists and conservation biologists have contributed to control of invasive plant species in natural ecosystems (termed “environmental weeds”) by communicating findings of observational and manipulative studies in weed-affected communities. Such research contributes to improved eradication, control or management techniques for environmental weed infestations (e.g. Vranjic et al. 2000b). However, publication of ecological findings alone will not achieve policy change. There is a human dimension to change that demands greater interdisciplinary communication among ecologists, conservation biologists and social scientists (e.g. Underwood 1996, Armsworth and Roughgarden 2001, Bradshaw and Bekoff 2001, Kinzig 2001). Ecologists must also interpret their data and conclusions rather than relying on policy analysts who may prefer political expediency (Norton 1998). This paper seeks to improve understanding by ecologists of the intrinsic human dimension of weed invasion and control. A strong socio-ecological

framework, which acknowledges and works with human behaviour, is crucial to success of weed control efforts.

This paper assesses aspects of current weed policy including characterisation of the weed issue, policy framing and implementation of instruments such as regulation, voluntary incentives, education and economic instruments. Resourcing and monitoring regimes are also analysed. Current instruments are compared with a generalised natural resource management policy framework adapted from Dovers (1995, 1999) and presented in Table 2.1. Author opinion regarding current utilisation of each weed policy component is also included in Table 2.1.

Table 2.1: Natural resource management policy framework (modified from Dovers 1995; 1999) applied to invasive species policy.

Policy component	Application of policy component*
Issue characterisation	
• Monitoring and understanding natural and human systems and their interactions	2
• Identification of environmental change and degradation	2
• Identification of relevant social goals and public concern	2
• Assessment of risk, uncertainty and ignorance	2
• Scaling and framing of policy problems	1
Policy framing	
• Identification of policy principles	2
• Development of policy statement	3
• Definition of measurable policy goals	1
Policy implementation	
• Selection and planning of policy instruments	2
• Provision of statutory, institutional and resourcing requirements	1
• Establishment of enforcement/compliance mechanisms	2
Monitoring and review	
• Mandated evaluation and review	1
• Policy monitoring	1
• Extension, adaptation, redesign or cessation of policy, as required	1

*Assessment of application of policy components is based on author opinion and is rated as follows:
1 = underutilised; 2 = moderately utilised; 3 = well utilised

The review focuses on environmental weed control in Australia with specific reference to the policy implementation phase. Case studies are drawn from the state of New South Wales (NSW).

Issue characterisation

The probability of dispersal and establishment of invasive plant species is dependent on human behaviour (Perrings et al. 2002): both transportation and industry aid propagule dispersal (di Castri 1989, Mack et al. 2000) while establishment and dominance of these species are often facilitated by human induced disturbance (Amor and Piggin 1977, Fox and Fox 1986, Hobbs and Huenneke 1992, Keane and Crawley 2002). Consequently, interactions between human and natural systems have allowed invasive plant species to exceed natural rates of range expansion. It is imperative to recognise the human dimension of weed invasion: human behaviour is largely responsible for rapid weed spread as well as weed control.

Considerable research effort has focused on the process, impacts and amelioration of weed invasion in natural ecosystems. Researchers have proposed mechanisms of invasion and modelled invasion processes (e.g. Hastings 1996, Rejmanek 1996, Davis et al. 2000, Naeem et al. 2000, Keane and Crawley 2002). Numerous studies have detailed direct and indirect weed impacts through altered primary productivity, species interactions and diversity, disturbance regimes and ecosystem processes (e.g. Vitousek 1990, Walker and Smith 1997, Mack and D'Antonio 1998, Mack et al. 2000, Yelenik et al. 2004). Finally, the management literature has detailed methods of controlling weed invasions (e.g. Buchanan 1995, Muylt 2001). Further research needs in Australia include determining thresholds of biodiversity decline following weed invasion, investigation of invasion mechanisms and understanding weed impacts on fauna (Adair and Groves 1998).

The main drivers of weed invasion are often well understood by scientific and management communities and control techniques have been developed for some invasive species. Residual uncertainty may be managed through consultation with researchers and implementation of monitoring regimes (see “Monitoring and review” section below). Indeed, weed control does not frequently require detailed population biology knowledge, and an absence of research should not excuse inaction (Simberloff 2003). As with much natural resource management, it is often ineffective political processes rather than a lack of knowledge that limit conservation outcomes (Dovers 1995, Walker et al. 2001). Insufficient public concern may partly explain ineffective political processes. The Cooperative Research Centre (CRC) for Australian Weed Management recently commissioned a study researching community awareness of, and attitudes towards, weeds as a significant national problem. Results indicated that urban focus-group participants did not understand the extent of the environmental weed problem (Market Attitude Research Services pers. comm. 2003). Such findings indicate a need for strengthened education, certainly amongst the majority, politically influential urban population. An informed and mobilised Australian public will facilitate better weed policy.

Appropriate scaling and framing of policy problems are important in effective weed control. Weed policy has often emphasised species-led rather than site-led work schedules. For example, the national strategy focuses effort on twenty identified Weeds of National Significance. Similarly state agencies devise strategies and allocate resources for regionally significant environmental weed species (e.g., NSW Bitou Bush *Chrysanthemoides monilifera* ssp. *rotundata* plan, Victorian Blackberry *Rubus fruticosus* agg. plan). A species-led approach facilitates clear prioritisation and allocation of resources, and may be the best approach for particular control techniques.

For example, the benefits of classical biological control (McFadyen 1998) are generally realised through target of a single weed species in the system. However, a species-led approach may result in equivocal ecological outcomes. Control of a target weed may facilitate expansion or secondary invasion by non-target weed species (Stockard et al. 1985, Pickart et al. 1998, Yelenik et al. 2004). Furthermore, state agencies frequently have different prioritisation criteria to manage individual weed species. An environmental weed may be prioritised for control in conservation reserves, but receive lesser control in water catchment or forestry landscapes. Consequently weed control may vary across tenures (Panetta and Lane 1996) and species may continue to invade managed areas from adjacent unmanaged or poorly managed infestations, ultimately reducing the effectiveness of agency control programs.

Successful weed control must address causes of invasion such as imposition or alteration of disturbance regimes (Fox 1991, Hobbs and Huenneke 1992, Hobbs and Humphries 1995), increased resource and propagule availability (Davis et al. 2000) and positive feedbacks where invaders are able to alter ecosystem function (Mack and D'Antonio 1998). Species-led policy directions take little account of these ecological findings and often treat the manifestation (i.e., weed invasion) of environmental degradation rather than the cause.

Alternatively, site-led weed control focuses on community or ecosystem dynamics rather than individual species. Examples of site-led weed control may be found at the local level: local community groups may control a suite of targeted weeds at a work site while also addressing disturbances such as high nutrient runoff and conducting post-control revegetation (e.g. Pallin 2000). Often, site-led weed control requires more labour and resource inputs per unit area than species-led control, which in turn results in reduced absolute area of control. Ultimately, utility of site- or species-led

control approaches should be decided by weed policy on the basis of conservation goals, resource availability and the circumstances of weed invasion.

Framing the solution

In Australia, the National Weeds Strategy (Anon. 1999) provides a framework for weed policy. The strategy recognises four main principles: (1) integrated weed management is necessary for sustainable development, (2) prevention and early intervention represent the most cost-effective forms of control, (3) weed management requires a national approach with involvement from all levels of government, and participation by industry and the community, and (4) landholders have primary weed control responsibilities, however collective action is required where weed invasion exceeds individual capabilities. Despite clear utility of these policy principles, they have not been widely implemented. Importantly, there is increasing recognition that a national approach to weed management, regulation and resourcing is lacking (Pannell 1999, Williams et al. 2001, Bartlett 2002). Although local, regional and state activity is vital in weed control, autonomy at these levels lacks strategic direction and national leadership is required.

Furthermore, the principle of early intervention has not been widely enacted. There is a need to implement a formalised rapid response system for weed species which breach quarantine or naturalised species displaying increased abundance. Such a system may apply eradication, containment or control at an early stage. The concept of sentinel sites or sentinel groups, under development at the CRC for Australian Weed Management, may address current policy deficiencies. Sentinel sites or groups are established to strategically monitor weed flora and alert control authorities to new incursions. Establishment of such sites or groups, properly resourced, may prove a

powerful management tool with important community awareness and education applications.

The first main goal of the national strategy is to prevent new weed problems in Australia. The remaining two goals target twenty nominated Weeds of National Significance (WONS): the strategy seeks to reduce current impacts of these weeds and provide a managerial framework to maintain control. While explicit prioritisation of the twenty WONS may aid in decision-making, it may not offer the best strategic approach (Williams et al. 2001). A national strategy must address all weeds which threaten biodiversity, especially emerging species.

The National Strategy sets a context for state and regional policy. State and Territory governments have developed weed strategies primarily to manage extant invasions. In turn, regional and local weed strategies have been developed to meet state priorities and guide on-ground work programs. While most strategies state goals and objectives, identify stakeholders and outline actions to meet proposed objectives, such documents often fail to appropriately resource actions and review progress. The review process requires comparison of outcomes with measurable goals and objectives. While some strategy documents provide quantitative goals and timelines (e.g., South East Catchment Blueprint: Anon. 2001a), in general weed strategies are overly generic. Weed policy requires ambitious, measurable goal setting, driven by increased political and community will to address the serious and continuing impacts of weed invasion.

Implementation

Selection of policy instruments

A number of policy instruments are available to achieve natural resource management and include regulation, voluntary incentives, education, information and motivational instruments, property-right instruments and pricing mechanisms (Young et

al. 1996). The following discussion addresses these instruments and evaluates their effectiveness in achieving weed control.

Regulatory instruments

Four tiers of law contribute to weed management frameworks in Australia, namely international, federal, state and local law. International law attempts to mitigate environmental weed invasion primarily through treaties (e.g., *Convention on Biological Diversity 1993*). However, the effectiveness of international environmental treaties may be undermined by economic imperatives. Australia is also a signatory to the *World Trade Organization Agreement on the Application of Sanitary and Phytosanitary Measures 1995* and the *Technical Barriers to Trade Agreement 1995*. These agreements support trade liberalisation and require member nations to substantiate all trade restrictions with scientific justification (Anon. 1995, Cameron and Campbell 2002). The aim of these agreements to globalise trade may also facilitate accelerated weed transport and establishment, in turn undermining international environmental conventions and federal quarantine legislation.

Australian federal legislation contributes to environmental weed management through enacting quarantine, providing a process of weed impact assessment and regulating the use of chemical and biological weed control. The ensuing discussion focuses on quarantine and conservation legislation. Quarantine legislation (*Quarantine Act 1908*) aims to provide an efficient and cost-effective initial mechanism of weed control with detection and prohibition of invasive species before they can establish and spread. The Australian Quarantine and Inspection Service (AQIS), has recently adopted a permitted species list to regulate plant imports. The system is intended to improve selectivity of national quarantine barriers and provide transparent, scientific justification for imposition of trade barriers. Species proposed for importation, which do not appear

on the permitted list (and which have not been previously prohibited), are subject to a Weed Risk Assessment, which is a pre-entry assessment of weed potential (Pheloung 2001). Weed potential is determined by scoring species according to historical, biogeographical, biological and ecological attributes (Pheloung 2001).

However, the Weed Risk Assessment (WRA) process has limitations. The system recognises high-risk attributes such as prolific seed production as good indicators of weed potential (Pheloung 2001). Yet the ability of such attributes to consistently predict which plant species will become weeds has been questioned (Hobbs and Humphries 1995, Enserink 1999, but refer also to Kolar and Lodge 2001). Lonsdale and Smith (2001) reported that the WRA was able to accurately distinguish weed species in 90% of cases for the Asteraceae, but only in 42% of cases for the Fabaceae. As such, quarantine barriers may be permeable to plant species with unrecognised invasive traits. Furthermore, as some genera are listed as permitted, it is possible for weedy species of a permitted genus, or weedy species with synonyms where the genus is permitted, to escape detection (Spafford Jacob et al. 2004). The risk assessment process cannot effectively screen for sleeper weed species. Sleeper weeds have a latent weed potential and may become invasive following altered disturbance regimes, changed pollination dynamics or evolutionary processes (e.g. Low 2002a). The interaction of plant imports with a novel and changing environment complicates quarantine risk assessment (Arcioni 2003) and ultimately reduces its effectiveness. Finally, quarantine legislation is limited to regulating declared plant imports. Illegal exchange of plant material facilitated by the internet (Kay and Hoyle 2001), international travel, postal services (Arcioni 2003) and accidental importation undermines extant legislation. Such limitations cannot be remedied by further law-

making. Rather, other social instruments such as research and education should be used to complement legislative controls.

The *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act) provides an environmental assessment and approval process for proposed actions with a likely significant impact on matters of national environmental significance or on Commonwealth land. The EPBC Act complements Australian quarantine legislation by regulating the import of live plants which may adversely affect native species or their habitats (Sect 301A). Presently, the EPBC Act focuses on preventing admission of potentially harmful weed species into Australia. However, there is little consideration of impacts wrought by established invasive weed species on native biodiversity. The impacts of feral vertebrate (Goat, Rabbit, Cat, Red Fox, and Pig) and invertebrate (Fire Ant) species have been recognised in the legislation through listing as Key Threatening Processes and consequent provisions for threat abatement planning, yet collective or specific weed invasion is yet to be recognised by the Commonwealth as a key threat to native biodiversity. Under the Act, regulations may be implemented where weed invasion directly threatens biodiversity, while bioregional planning, bilateral agreements and management plans for Commonwealth reserves are available as indirect control measures. However, at present these legislative controls have not been utilised (Arcioni 2003).

Current deficiencies in the legislation may be remedied by the *Environment Protection and Biodiversity Conservation Amendment (Invasive Species) Bill 2002* under consideration by parliament. The Bill seeks to explicitly control and manage invasive species at the federal level with particular reference to regulation of potentially invasive imports and management of eradicable or containable invasive species. The

Bill signals a need for increased Commonwealth assistance and involvement both in preventing further incursions and managing extant invasive species.

State and Territory legislation regulates operational and planning mechanisms of weed control. These legislative instruments are important components of weed control as they deliver greater compliance than market-based incentives (Young et al. 1996). However, regulation does have limitations. A report by Glanznig and Kessal (2004) found inconsistencies across State and Territory legal frameworks for control of invasive plants of national importance. Consequently, strong trade, sale or import restrictions along with eradication or control mechanisms in one State may be undermined by poor mechanisms in adjacent States (Glanznig and Kessal 2004). Similarly, the primary NSW weed legislation (*Noxious Weeds Act 1993*) suffers from inconsistent application within the State across land tenure. The Act states that public authorities are only required to control weeds “... to the extent necessary to prevent them from spreading to adjoining land” (Section 13). Such requirements contrast with obligations on private land occupiers who must actively control noxious weeds according to proclaimed control categories. Public authorities manage much of the land dedicated for conservation purposes in NSW, yet the limited powers of the Act on these public lands (Panetta and Lane 1996) results in inconsistent control across political boundaries.

Enforcement of the *Noxious Weeds Act* must also be considered. Generally, compliance in the case of public authorities is sought through negotiation. However, enforcement procedures for private occupiers follow a path of increased sanctions from penalties to legal action for cost recovery (Arcioni 2003). Local Control Authorities (LCAs) have on-ground weed control functions and consist of a single council of a local government area or multiple councils forming a county council. At present, enforcement

is limited by the ability or will of Local Control Authorities to routinely inspect districts, ignorance of occupiers (and sometimes inspectors) regarding weed identity and status, and high costs and evidentiary burdens of prosecution proceedings (Arcioni 2003).

State legislative controls may be inadequate or inappropriate in addressing large-scale weed incursions. For example, Lantana *Lantana camara*, a shrub native to South America, has invaded four million hectares in northern and eastern Australia. It has been declared a Weed of National Significance due to its impact on agriculture and native systems (ARMCANZ 2000). Lantana is most problematic in coastal, high rainfall districts, yet only three coastal NSW LCAs have declared the species as W2 (requiring full and continuous suppression and destruction) under NSW legislation. A further six LCAs have declared the species as W3 (requiring prevention of spread to reduce numbers and distribution) and the remaining ten coastal LCAs have not declared Lantana as noxious, thus do not have an obligation to control the species. Inconsistent application of control categories under the *Noxious Weeds Act 1993* may reflect variable resources, commitment and extent of invasion across LCAs (NWAC 2002). However, inconsistencies across LCA boundaries coupled with contrasting national and state priorities may waste limited control resources. Lantana invasion may exemplify an environmental weed which is beyond eradication and perhaps containment. Ultimately the best strategic outcome may be to abandon legislative control of such large-scale weed incursions and focus resources on specific invasion of high conservation value sites or other manageable weed problems.

Legislators and policy makers must recognise that the dispersal syndrome of weed species influences the utility of regulation. Weeds utilising predominantly human mediated dispersal mechanisms, such as invasive pasture species (Lonsdale 1994), are

more likely to respond to legislation than weeds that do not rely on human vectors for dispersal (Panetta and Scanlon 1995). Importantly, many environmental weeds use non-human dispersal vectors such as birds and other vertebrates (e.g., Bitou Bush and Camphor Laurel *Cinnamomum camphora*). Regulation through the *Noxious Weeds Act* therefore inadequately controls these environmental weeds, and other instruments such as voluntary incentives (see below), become more important in controlling the extent and density of invasion.

NSW legislation, which defines local government roles in environmental weed control, includes the *Local Government Act 1993* (LG Act) and the *Environmental Planning and Assessment Act 1979* (EPA Act). Under the LG Act, weed control may be achieved through plans of management for different land classifications (Arcioni 2003). Planning instruments under the EPA Act, namely State Environmental Planning Policies, Regional Environmental Plans and Local Environmental Plans, may assist weed control through zoning provisions and development constraints. Although planning instruments represent an important potential mechanism of weed control, such mechanisms are not well utilised at the local level (Arcioni 2003). Mamouney (2000) provides some insight into potential reasons for poor implementation of available local instruments in biodiversity management. The author cites factors such as competing functions where local governments provide both development opportunities and biodiversity management, a dominant service-provision culture, influence of business and wealthy individuals and institutional and organisational hurdles as impediments to effective biodiversity management (Mamouney 2000). As a result, local mechanisms of environmental weed control may be underutilised.

Overall, diverse legislative instruments are available in regulating weed control. However factors such as competing goals amongst international treaties, deficiencies in

current predictive powers of federal quarantine and inconsistencies and underutilisation of extant federal, state and local weed regulatory mechanisms mean that other social instruments must be employed to address control deficiencies.

Voluntary incentives

Voluntary incentives rely on voluntarism and self regulation rather than coercion or financial incentives (Young et al. 1996). Voluntary participation, through formal and informal projects such as “Coastcare”, “Bushcare”, “Landcare” and “Friends of” groups, is an important labour component of weed control in Australia. Actual voluntary contributions to weed control are unknown, but a study by Sinden et al. (2004) found that volunteer effort for particular projects can be significant. For example, a community group working in a 30 ha site along the Avon River in Western Australia provided an estimated 1 698 hours over 10 years for the control of woody and other weeds (Sinden et al. 2004). Voluntary incentives have the advantage of inducing a strong multiplier effect for initial in-kind and monetary contributions from government, local organisations and individuals (Young et al. 1996, Margerum 1999).

However, in order to work effectively, volunteer programs require active government support. Often community groups feel marginalised if they are omitted from consultative processes concerning development and land use within or adjacent to their worksites. Development of formal agreements or partnerships between land management agencies and volunteer groups may provide recognition of volunteer effort and ensure local planning and weed control are aligned.

Furthermore, volunteer effort is often poorly resourced. Volunteer effort frequently requires coordination and local technical and ecological expertise. Indeed, issues such as misidentification of native species as weeds (Taylor 1995) have been reported as problems with community weed control activities and highlight a need for

strong coordination and supervision of community and individual weed control action. Extension officers provide coordination and supervision skills and are represented in federal, state and local agencies. Extension officers are an important link between education and implementation and often facilitate learning through informal, face-to-face conversations, a method which has been demonstrated as highly effective (Westley 1995). There has been a general trend in natural resource management of a reduction in staff and resources for traditional extension services (Cullen et al. 2001). I believe the role of extension officers is increasingly important in a political climate of small-scale works funding and reliance on local, volunteer effort. Officers link policy with on-ground work by directing local community effort to conform to extant reserve-specific and larger scale weed management policies and plans.

Another important use of voluntary incentives in effecting weed control is through development of voluntary standard-based accreditation of businesses (Young et al. 1996). Standard-based incentives have considerable potential in combating horticultural promotion and propagation of environmental weeds. Findings by Groves et al. (1997) that 65% of introduced species naturalised in Australia between 1971 and 1995 were introduced as ornamental species, indicate the importance of addressing horticultural practices. The Bushland-Friendly Nursery accreditation system, introduced on the north coast of NSW (www.fncw.nsw.gov.au/nursery), is one example of voluntary standard-based incentives. Participant nurseries do not sell listed aggressive environmental weeds and receive “bushland-friendly” accreditation. Such a system signals increased cooperation and communication between the horticultural industry, local government and consumers, and provides an initial mechanism in addressing the ongoing problem of introduction and assisted dispersal of environmental weeds through

horticulture. However, it is likely that such ventures will require a legislative framework in the long-term to ensure comprehensive control.

Education, information and motivational instruments

Environmental education provides a powerful long-term mechanism for raising public awareness and facilitating attitudinal change. Education links ecology and social science to facilitate adaptive management - an iterative process of learning about a dynamic system and designing and monitoring experiments to determine optimum management regimes (Walters 1997, Shea et al. 2002).

In general, education relating to invasive species has been tenuously linked to the primary and secondary environmental education portfolio. Weed education in the public school system is often dependent on the interests and resources of individual schools (Kwong 2002), which may limit learning outcomes. However, in NSW, invasion ecology is now an option in the Earth and Environmental Science Higher School Certificate course (http://hsc.csu.edu.au/earth_environmental/options), signalling improved secondary school weed education initiatives. Provision of weed education in the school system may achieve on-ground weed control through practical learning, sharing of learning experiences in the home (Margerum 1999), and development of skills for future land managers and policymakers.

Formal weed education also extends to technical and vocational coursework with provision of training and accreditation to weed managers, weed control officers, bush regenerators and extension officers (e.g. Carter et al. 2002). Research bodies such as the CRC for Australian Weed Management, provide collaborative ventures between industry, universities and government departments. The CRC supports weed research, education and extension programs and provides undergraduate, postgraduate and postdoctoral positions in environmental weed management (Williams and West 2000).

The informal education system delivers weed management information to the wider community. Considerable educational material has been developed in Australia over the past decade with the intent of increasing awareness and activity in weed control. For example, “National Weedbuster Week” increases the profile of weeds through distribution of weed products, promotion of weed issues in the media, organisation of activities and promotion of community groups involved in weed control (Vitelli et al. 1999). Furthermore, field days, exhibitions and demonstration sites showcase weed control techniques and outcomes thus providing practical learning experiences for individuals and community groups. Electronic media through the internet and email discussion groups provide further weed ecology and control information. Finally, television, radio and print media communicate research developments and impacts of environmental weeds. For example, environmental weed issues have received exposure in popular science literature (e.g. Low 2001, Low 2002b) and in national television advertisement campaigns focused on quarantine (AQIS “Quarantine Matters” television advertisement campaign).

Strong educational initiatives and extension services may ameliorate deficiencies in weed funding. For example, on the north coast of NSW, short term federal funding (Natural Heritage Trust grants) has been directed towards formal training of community group representatives in weed control techniques rather than on-ground works (R. Joseph pers. comm. 2002). Such schemes improve the standard of control operations and group autonomy, which in turn may combat future funding vagaries. Policy must aim to appropriately skill and support local volunteer groups which will promote local ownership of the weed problem.

Further motivational instruments may include auditing systems and provision of awards (Young et al. 1996). Audits may both assess the performance of local control

effort and evaluate the impacts of various land uses in an area. Weed auditing requires record-keeping capabilities (e.g., through mapping systems). Although costs are involved in establishing such systems, they have the dual utility of facilitating audits and contributing to monitoring requirements (see “Monitoring and review” section below). A system of prizes or awards may then be coupled with weed audits to encourage behavioural change, generate publicity for weed issues and reward control effort.

Property-right instruments and pricing mechanisms

Property-right instruments such as covenants, management agreements and offset arrangements may be particularly important in providing weed control on private land. Land covenants restrict landowner activities (e.g., clearing) with the intent of protecting biodiversity values. Covenants may apply for a fixed term or operate in perpetuity and landowners commonly receive payment for entering into such agreements (Young et al. 1996). Covenants may indirectly achieve weed control through preserving natural vegetation and reducing human-induced disturbance. In contrast, management agreements may achieve direct weed control as landholders receive reimbursement for capital and incremental costs of providing non-marketable biodiversity services such as weed removal (Young et al. 1996). Management agreements have particular merit in protecting existing remnants from ongoing weed invasion and consequent degradation of biodiversity values. However, it is desirable to attach a conservation covenant to land under management agreements to improve the likelihood of permanent conservation (Young et al. 1996). Offset arrangements are another property-right instrument which may be applicable to weed control. Industry may offset the damage it causes by reclaiming or regenerating an equivalent degraded land area elsewhere (Young et al. 1996). One example of offsetting may be developer-

funded weed control and regeneration of remnants adjacent to proposed developments as a condition of consent – such arrangements have been applied to a housing estate development in coastal northern NSW (R. James pers. comm. 2004). However the ability of offset arrangements to attain biodiversity values of undisturbed vegetation and achieve industry compliance may be limited as illustrated by assessment of wetland mitigation projects in the United States of America (e.g. Simenstad and Thom 1996, Sudol and Ambrose 2002).

A number of pricing mechanisms exist which may be useful in environmental weed control on both public and private land. Where weed invasion results from resource extraction activities such as sand mining, performance bonds may be imposed on the user. A regulatory body secures a bond from the user which is returned on completion of the activity unless bond conditions are breached (Young et al. 1996). Inclusion of weed control requirements in performance bonds may contribute to ecosystem resilience and assist ecologically meaningful restoration. However, performance bonds are temporary measures and do not address weed invasion that manifests with time since disturbance. Charges, levies and use fees may also be applied to raise revenue for weed control in conservation reserves. In keeping with the “user pays” principle, charges, levies and fees are directed at those who enjoy and use biodiversity (Young et al. 1996). Imposition of a charge system does incur collection costs which, coupled with monitoring and enforcement, may reduce its effectiveness and efficiency (Young et al. 1996, Hawkins 1999). Furthermore, site-specific charge systems may not sufficiently finance control operations in low-visitation reserves. Finally, tax deductions and rate rebates may be used to reduce costs of undertaking weed control activities, particularly on private land.

Importantly, property-right and pricing instruments such as management agreements and taxation are best implemented as incentives rather than sanctions (Bowers 1999) as the landholder has an interest in protecting his/her income and therefore maintaining conservation. Furthermore, careful monitoring and swift update of economic instruments are required when economic circumstances change. For example, if agricultural produce prices rise, a landholder may preferentially clear or degrade remnant vegetation despite imposition of fines, as the agricultural option has become more profitable. If instruments are to achieve conservation outcomes, compliance must remain the most profitable option for landholders (Bowers 1999).

To date, property-right and pricing instruments have not been widely used in achieving environmental weed control and there is little empirical evidence of the utility of these mechanisms in delivering positive biodiversity outcomes (Young et al. 1996). However, market-based incentives may prove more cost-effective and efficient while being less intrusive in comparison with regulatory systems and warrant further investigation by weed policy makers.

Provision of resources

Economic resources fund operational programs, salaries, planning, research, education and extension services. Despite significant voluntary and industry contributions, it is federal, state and local government funding that drives weed programs, and allocation of these public monies is the subject of the ensuing economic discussion.

Sinden et al. (2004) documented the most comprehensive recent estimate of the economic impacts of weeds in Australia. The report found that weed control expenditure by national, state and territory bodies in natural environments was at least \$19.597M for the 2001-02 financial year. A further \$80.775M was conservatively

expended on weed management activities by public authorities and public land managers in the same financial year, while expenditure on indigenous land in the Northern Territory was estimated conservatively at \$3.045M per annum between mid 1998 and mid 2003 (although funds provided for public and indigenous lands may not exclusively control environmental weeds). Commonwealth expenditure on weed management and research during the 2001-02 financial year was at least \$8.252M (Sinden et al. 2004). Environmental weed expenditure may be compared with control costs in agriculture. Sinden et al. (2004) estimated that farmers invested at least \$1 365M in agricultural weed control for the 2001-02 financial year. The significantly higher investment in agricultural *versus* environmental weed control reflects the fact that agricultural weed control is an internal cost in the market system: individual farmers bear the majority of weed control costs, but also experience most of the benefits through increased production. So the market system is able to achieve reasonable control of agricultural weeds. In contrast, environmental weed control represents an external cost. Attributes of uninvaded natural systems remain unpriced in the market system: control does not provide a direct benefit to individuals so there is little incentive for the market system to ensure adequate control. Consequently significantly fewer funds are directed at control of environmental weeds when compared with agricultural weeds.

Little information exists on impacts of weed invasion on unpriced attributes of native ecosystems. Such attributes include biodiversity, ecosystem services, habitat provision and amenity (Naylor 2000, Vranjic et al. 2000b). Economic valuation tools such as benefit-cost analysis have been developed to account for and internalise unpriced environmental resources into the market system (Turner et al. 1994). Economic valuation has been used as an incentive for conservation of environmental

resources in numerous case studies. For example, studies in hypothetical South African fynbos ecosystems have demonstrated the cost-effectiveness of controlling weeds to maintain services such as water production and genetic storage (van Wilgen et al. 1996, Higgins et al. 1997). In Australia, Odom et al. (2003) used a dynamic optimisation model for Scotch Broom *Cytisus scoparius* management within a national park.

Furthermore, a study by Sinden et al. (2004) quantified the value of protecting threatened species from weed invasion. Such modelling has applications in benefit-cost analyses where biodiversity protection is an objective of weed management.

Comprehensive analysis of costs associated with controlling environmental weeds may set a benchmark for realistic funding and inform policy on appropriate management options.

Although the total economic impacts of managing environmental weed invasion in Australia have not been calculated, it seems clear that current funding levels are inadequate because policy goals are not being met. For example, bitou bush, introduced from South Africa, has successfully invaded coastal vegetation communities in NSW. Annual expenditure in NSW on bitou bush control has been estimated at \$2M (CRCWMS 2001). Despite this funding, anecdotal evidence suggests that bitou bush infestations continue to spread at a rate of 1 to 5% per year (CRCWMS 2001). Bitou bush is a Weed of National Significance (WONS). As discussed above (“Framing the solution” section), the National Strategy seeks to reduce current impacts of WONS, however extant funding provisions are insufficient to meet the stated strategy goals. Ultimately, funding magnitude dictates the utility of other policy instruments such as legislated Threat Abatement Plans (NSW), educational campaigns and extension support.

Government funding of environmental weed control is generally short term (typically 1 year funding cycles) and projects receive no guarantee of continued assistance (Panetta and Lane 1996). Short term funding results in unambitious weed control programs: land managers may reduce the scope of operations to safeguard against over-commitment if funding is not renewed in the next cycle. The inadequacy of funding durations is clear when considering the longevity of viable propagules for many significant environmental weeds. For example, research on Gorse *Ulex europaeus* in New Zealand indicates that seed of this species may survive in the soil seed bank for over 10 years depending on burial depth and location (Hill et al. 2001). If control programs of such long-lived weed species are to achieve success, funds must be available to ensure follow-up work continues until the viable weed seed bank is exhausted.

Environmental weed control has received minor funding relative to other natural resource management issues. For example, it is estimated that invasive plant control programs receive less than 10% of funds currently allocated to amelioration of salinity (Martin 2003), another major land degradation issue in Australia. Significant, detrimental impacts of environmental weed invasion on biodiversity conservation require prioritisation of weed control at the federal level (Anon. 2001b). The urgency of a federal funding review is compounded by findings that viability and cost-effectiveness of weed control are greatest in early stages of the invasion process (Hobbs and Humphries 1995, Panetta and James 1999, Smith, HA et al. 1999).

Monitoring and review

Analysis and review of natural resource management programs and policies are critical to successful outcomes (Dovers 1995, Curtis et al. 1998, Bellamy et al. 2001). Program assessment should determine the utility of goals and objectives, evaluate

methodologies, establish whether proposed activities were undertaken and determine whether program outcomes achieve stated objectives (Curtis et al. 1998). Monitoring and review may improve understanding of the relative costs of different management scenarios (Christensen et al. 1996). Procedures may include field audits, assessment of progress against deadlines and stakeholder feedback. In Australia, while some state and territory weed strategy documents recognise monitoring and review as important in policy evolution, none of the current weed strategies provide measurable performance indicators for stated actions. Consequently, there is relatively little evaluation of weed management strategies (Grice 2004), and it is difficult to assess the success of policy initiatives in weed control.

Current record keeping and monitoring processes advocated by strategy documents are rarely completed satisfactorily, and natural resource management staff members are frequently reluctant to challenge the existing culture of poor reporting (Curtis et al. 1998). Increasingly landholders and community groups are required to fulfil monitoring and record keeping responsibilities. However, time constraints and training deficiencies have resulted in insufficient data collection, poor analysis and superficial application of weed invasion and control data (refer to Briggs 2003 for related discussion).

In order to achieve meaningful monitoring and evaluation of weed control effort, policy makers must recognise the importance of good quality data collection, storage and analysis in achieving adaptive weed management. A number of factors must be considered in improving current monitoring and evaluation procedures. Firstly the study aims and goals must be clear and appropriate to then direct data collection and analysis. The scientific community has much to offer in terms of developing rigorous monitoring methodologies, particularly sampling design, statistical analysis and modelling

(Christensen et al. 1996). Secondly, agencies must prioritise monitoring of weed control by employing data managers and training staff and community group representatives in good quality data collection and entry. For example, in Queensland's Herbert River Catchment, a Geographic Information System has been developed with guaranteed stakeholder involvement. The system facilitates collection, storage maintenance and analysis of catchment data (Walker et al. 2001). However, the Herbert River Catchment experience points to a need for external agency assistance in development and use of such databases and natural resource decision-making tools (Walker et al. 2001). Thirdly, monitoring and evaluation systems must be maintained over relatively long political timeframes (i.e., 5-10 years) (Dovers 1999) to understand the response of natural systems to weed control activities. Indeed, Dovers (1995) argues that strong statutory and institutional frameworks must underpin collection and communication of environmental information. He asserts that independent, mandated institutions such as the Australian Bureau of Statistics provide a model for development of environmental information. Finally, program monitoring must link back to policy formulation and inform future policy directions (Dovers 1995). Agencies who deliver weed policy must be just as much a part of the evaluation process as the on-ground program participants (Bellamy et al. 1999). Implementation of policy monitoring now will facilitate future policy analysis and improve cost-effectiveness of the process (Dovers 1999).

The outcomes of program and policy monitoring and evaluations should be communicated beyond the project stakeholders through peer-reviewed publication of findings (Curtis et al. 1998). Communication of findings allows managers to utilise best practices in weed control and allows the scientific community to deliver research findings relevant to on-ground management (Christensen et al. 1996).

Conclusion

The environmental weed problem is well understood by scientific and management communities. However, it appears this information is not filtering to public fora – a link which is crucial in increasing political will to drive effective weed control. In turn, while important policy principles have been developed to combat weed invasion, they require greater enactment, for example, through increased national leadership and prioritisation of rapid response systems to new weed incursions.

A number of policy instruments currently deliver weed control in Australia: regulation, economics, research and moral suasion provide important complementary control. However, economic instruments of property-right and pricing mechanisms warrant further development, while education and voluntary incentives require a strong extension service to maintain involvement and standards of control. Paramount to successful weed control is provision of sufficient and timely resources to support on-ground projects and meet strategy goals. As with many natural resource issues, weed control requires increased financial commitment from all government tiers. Release of significant funds is required to resource long-term weed control and restoration projects. Finally, monitoring and review of weed projects requires stronger implementation. Monitoring is an important link in adaptive management and improved policy making. Monitoring systems may be improved by setting measurable goals and providing standardised, user-friendly data collection and analysis infrastructure for weed managers.

Effective policy characterisation, framing, implementation and review will ultimately influence human behaviour and improve management outcomes. There is considerable opportunity for ecologists, conservation biologists and social scientists to collectively inform weed control strategies. Interdisciplinary cooperation should be encouraged to ensure strategies are effective, relevant and practical.

Chapter 3

Management regimes for a plant invader differentially impact resident communities

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Management regimes for a plant invader differentially impact resident communities.
Biological Conservation

Introduction

Plant invaders adversely affect key components of biological diversity including species diversity (French & Eardley 1997; McKinney & Lockwood 1999; Collinge et al. 2003), functional and guild diversity (Braithwaite et al. 1989; Holmes & Cowling 1997a) and ecosystem processes (Gordon 1998; Lindsay & French 2004). In addition, considerable socio-economic impacts of plant invaders have been reported (Mack et al. 2000; Pimentel et al. 2000; Sinden et al. 2004; Mason et al. 2005). Invader impacts are evident in most ecosystems and invasion represents a major and cosmopolitan conservation challenge for land management agencies.

Disturbance is a disruption of population, community or ecosystem structure and results in changed resource availability (White & Pickett 1985). Disturbance events create opportunities for new individuals to become established (Sousa 1984).

Management techniques which manipulate invader densities, create disturbance.

Management techniques are typically labour-intensive or land-extensive. Labour-intensive techniques involve considerable on-ground works where targeted exotics, at all life stages, are selectively removed via activities such as hand pulling and direct application of herbicide to cut stumps or foliage. This approach may involve on-ground localised disturbance with soil compaction, root disturbance, trampling and mechanical removal, however, the targeted approach of intensive management may release adjacent natives from invader impacts with minimal damage to native standing biomass. The

impact of intensive management techniques on biodiversity indices has been assessed in small-scale manipulative experiments (e.g. Snow & Marrs 1997; D'Antonio et al. 1998; Pickart et al. 1998), however, at large spatial and temporal scales, intensive management is enacted predominately by volunteer community groups with little formal monitoring. In contrast, land-extensive techniques prioritise large-scale reduction of invader biomass through techniques such as aerial application of herbicide or fire application. This approach avoids on-ground disturbance and high labour costs associated with intensive management, but is non-selective and affects both target and non-target species in the plant community.

Physical and biotic disturbance associated with both intensive and extensive management techniques may cause fluctuations in resource availability (Davis et al. 2000). For example, light resources increase with removal of an invader canopy and nutrient or moisture resources may be released through mortality or damage of native or invader individuals. Increased resources may be sequestered by both native and invader species, but high invader propagule pressure may favour invader dominance in the post-disturbance environment (Williamson 1996). The amplitude in resource fluctuation and intensity of propagule pressure may depend on the type of management, implicating the choice of management techniques in controlling future community invasibility.

I considered that a “successful” management technique would result in plant communities similar to the reference native state in species richness and structure (Aronson et al. 1993; McCoy & Mushinsky 2002). However, evaluation of invader management has generally been measured using administrative parameters (see Wilkins et al. 2003 for a related discussion) such as funding levels, area treated and degree of community commitment (but see Ogle et al. 2000). These administrative measures do not indicate whether management restores reference native conditions. Rather,

evaluation of management techniques requires rigorous scientific protocols (Chapman & Underwood 2000; D'Antonio et al. 2004) using biodiversity indices such as species richness and composition to compare managed communities with reference native communities.

This study evaluated the ecological success of intensive and extensive management regimes in controlling bitou bush (*Chrysanthemoides monilifera* ssp. *rotundata* (D.C.) Norl.), a South African shrub which invades fore and hind dune coastal communities. Bitou bush (hereafter termed bitou) was introduced to Australia in the early twentieth century. It was recognised as an effective sand stabiliser and actively planted in coastal New South Wales. Its invasive properties were recognised by the 1970s and deliberate dispersal was replaced with control regimes (Weiss et al. 1998). Fore dune control methods include both labour-intensive (primarily targeted) and land-extensive (primarily non-targeted) control. While aerial application of herbicide has occurred in hind dunes, it has limited effectiveness and control methods are typically labour-intensive. Bitou control programs have been operating for over a decade in some dune communities and ecological evaluation of control is timely.

In this study, I examined the effects of disturbance associated with different management regimes on the biodiversity value of dune communities. I examined community response with reference to both disturbance intensity and community type. I used non-invaded and bitou-invaded communities as references for the extremes of biodiversity value. I predicted that:

1. Intensive management which targets removal of the invader and minimises native damage provides better biodiversity outcomes as measured by species richness and composition indices than extensive management in fore dune communities,

2. Management in hind dune communities improves biodiversity outcomes as measured by species richness and composition indices such that managed sites are intermediate between non-invaded and bitou-invaded sites,
3. All management activities reduce invader cover and therefore reduce regeneration potential in managed compared with bitou-invaded sites.

Methods

Study area

The study area traversed the New South Wales coastal dune system (28° 12' 14" S; 153° 34' 04" E to 36° 57' 37" S; 149° 56' 07" E) which has been subject to widespread bitou invasion (Love 1984) and long-term control effort. The study area covered approximately 1 330 km of coastline and extended up to 1.4 km inland from the beach interface (Figure 3.1). Soils in the study area were derived from marine sands. Fore dune soils were generally comprised of siliceous sand with poorly developed profiles, while hind dune soils were sand podsols and exhibited comparatively more developed soil profiles with higher organic components (Conacher & Stanley 1991).

Fore dune sites were sparse to closed shrubland (Walker & Hopkins 1990) located up to 10 m within the fore dune shrubline, excluding incipient dune grassland communities. Typically, the tallest stratum comprised shrubs of *Acacia longifolia* ssp. *sophorae* with occasional isolated emergents of *Banksia integrifolia* or *Casuarina equisetifolia*. Common mid-stratum species were *Hibbertia scandens*, *Stephania japonica* and *Lomandra longifolia*, while the lower stratum was dominated by grasses such as *Zoysia macrantha* and *Spinifex sericeus* (Figure 3.2).

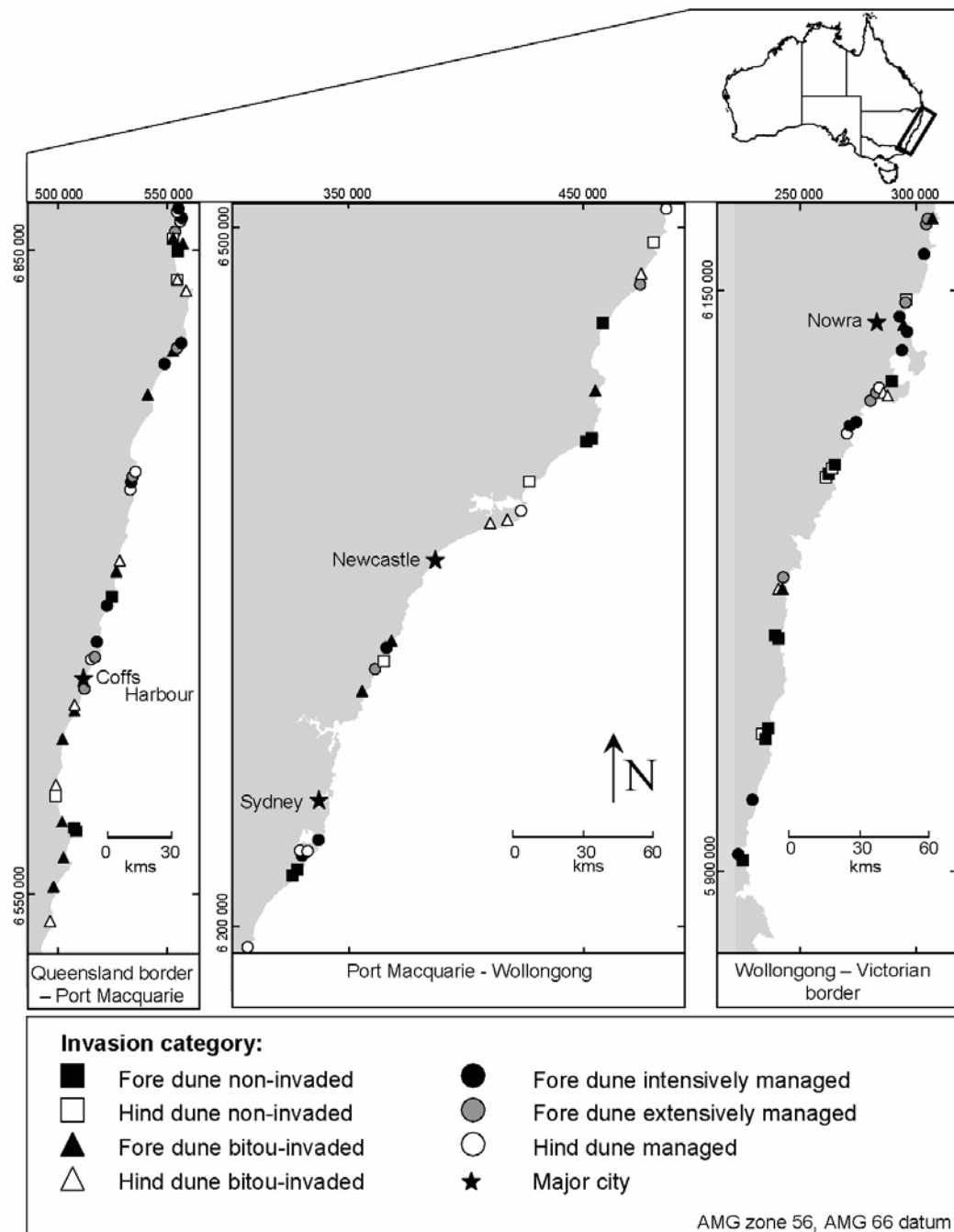


Figure 3.1: Location of non-invaded, managed and bitou-invaded fore and hind dune sites along the New South Wales coastline.

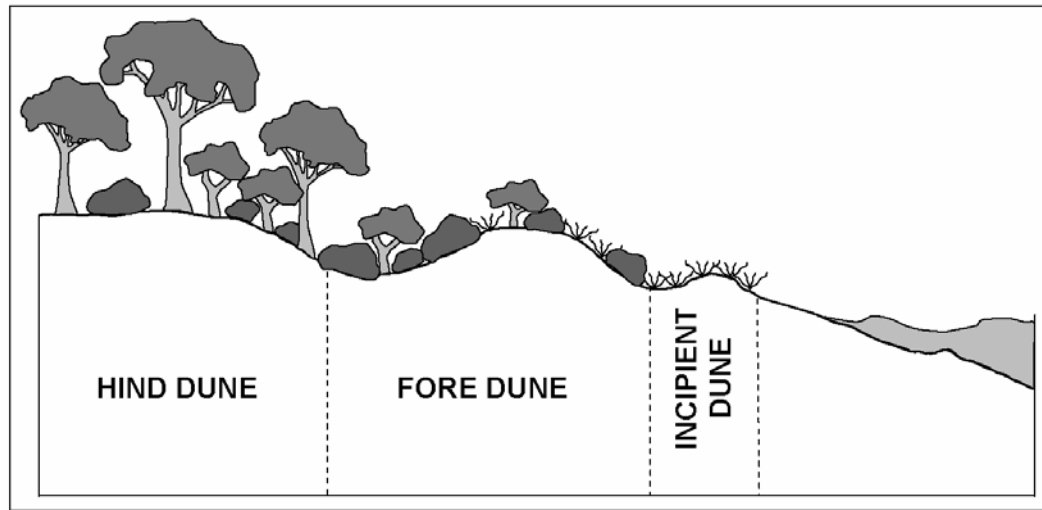


Figure 3.2: Schematic diagram of the fore and hind dune profile and associated vegetation communities (adapted from DLWC 2001).

Hind dune study sites were in woodland or forest communities (Walker & Hopkins 1990) and were established at least 5 m (generally >20 m) inside the treeline. The overstorey was dominated by tree species such as *Eucalyptus pilularis*, *Banksia integrifolia* and *Cupaniopsis anacardioides*. Common mid-stratum species were *Monotoca elliptica*, *Alectryon coriaceus* and *Acmena smithii*. The lower stratum commonly included *Pteridium esculentum*, *Lomandra longifolia* and *Themeda australis* (Figure 3.2).

Sampling methods

Interspersed sampling was conducted throughout the study area between September 2002 and May 2003. Sites were randomly positioned 20 x 50 m (0.1 ha) quadrats, which were considered a representative size for sampling community-level information (Rice & Westoby 1985). A nested 20 x 20 m quadrat was used to measure species abundance and environmental variables. I recorded vascular plant species rooted within and overhanging the 20 x 20 m quadrat. I excluded ephemeral geophytes due to considerable temporal variation in the survey period. Species nomenclature followed

Harden (1992; 1993; 2000; 2002). Percent foliage cover was estimated and a cover-abundance category was assigned using a modified Braun Blanquet scale (1, <5% cover and one or a few individuals; 2, <5% cover and uncommon; 3, <5% cover and common; 4, <5% cover and very abundant; 5, 5-20% cover; 6, 21-50% cover, 7, 51-75% cover and 8, 76-100% cover) (adapted from Poore 1955)). Cover values for bare ground, standing dead vegetation, litter and log (horizontal boles >10 cm diameter) and average litter depth were also recorded.

In the 20 x 50 m quadrat I recorded any new species not encountered in the 20 x 20 m plot, the presence of non vascular plant species (bryophytes), lichens, slope, aspect and distance (m) to strandline. Time since the most recent fire and occurrence of sand mining, along with details of control methods were obtained via a land manager survey which was distributed to representatives of public agencies and community groups involved in dune conservation and restoration. While reliance on land manager recollections is imperfect, limited public records of disturbance and control histories precluded more formalised approaches. Fire disturbance information was verified in the field by observation of understorey structure, leaf litter depth, presence and freshness of fire scars and age / size of fire sensitive plant species. Sand mining disturbance was verified with observation of dune profiling. The environmental, disturbance and invasion attributes used in the analysis are described in Table 3.1. Duration and frequency of management were variable, however in general, management duration was < 10 years and follow up occurred at least every 2 years.

Table 3.1: Description of environmental, disturbance and invasion attributes used to model species richness and bitou seedling abundance of coastal dune vegetation.

Attribute	Code	Code level	Attribute	Code	Code level
<i>Disturbance</i>			<i>Environment</i>		
Bitou cover	BIT_COVER	(0) absent (1) <5% cover (2) 5-50% cover (3) 51-100% cover	Season of survey	SEASON	(1) spring (2) summer (3) autumn
Time since fire	FIRE	(0) <5 years ago (1) >5 years ago	Aspect	ASPECT	(1) 135° - 225° (2) 45° - 135 (3) 315° - 45° (4) 225° - 315°
Sand mining	MINING	(0) absent (1) present	Longitude	LONG	Continuous variable
Litter depth	LITTER_DEPTH	(1) 0-5cm (2) 6-10cm	Latitude	LATIT	Continuous variable
			Distance to strandline	STRAND	Continuous variable –metres from each quadrat to the vegetation limit on the beach interface
			% cover bare ground	% BARE	Continuous variable
			% cover standing dead vegetation	% ST_DEAD	Continuous variable
			% cover litter	% LITTER	Continuous variable
			% cover logs	% LOG	Continuous variable
			% cover litter	% LITTER	Continuous variable
			% cover logs		
<i>Fore dune invasion category</i>					
	INVASION CATEGORY	(1) Non-invaded: no active control activities; average 5% bitou cover (2) Intensively managed (INTENSIVE): on-ground, targeted control of bitou individuals via hand removal, cut & paint of stems, backpack spraying etc. Considerable localised physical disturbance of site. (3) Extensively managed (EXTENSIVE): remote, non-targeted control of bitou individuals via aerial application of herbicide. Little localised physical disturbance of site. (4) Bitou-invaded: no active control activities; average 60% bitou cover			
<i>Hind dune invasion category</i>					
	INVASION CATEGORY	(1) Non-invaded: no active control activities; average 5% bitou cover (2) Managed: active control of bitou invasion through chemical and/or physical removal (3) Bitou-invaded: no active control activities; average 60% bitou cover			

In fore dune communities, four invasion categories were identified: (1) sites which had little bitou cover (average of 5 %) and no history of control activities: these sites were termed “non-invaded” (n = 17); (2) sites which had active control of bitou invasion via targeted, labour-intensive methods such as hand removal and direct application of herbicide (mostly glyphosate) to stems or foliage: these sites were termed “intensively managed” (n = 19). Limited aerial herbicide application occurred at some intensively managed sites, however these sites were included because intensive control dominated the management regime; (3) sites which had active control of bitou invasion mostly via non-targeted land-extensive aerial spraying (mostly glyphosate) programs: these sites were termed “extensively managed” (n = 13) and (4) sites which had high bitou cover (average of 60%) and no history of control activities: these sites were termed “bitou-invaded” (n = 16). Although non-invaded sites were not pristine, they were the least disturbed in the study area and the best representatives of original reference dune communities (Aronson et al. 1995).

In hind dune communities, 10 non-invaded, 12 managed and 12 bitou-invaded sites were surveyed. Management at hind dune sites could not be divided into intensive and extensive regimes due to low replication of extensively managed sites. Consequently, I chose to examine all managed hind dune sites in one management category. At most sites, control activities were intensive and included activities such as backpack spraying, direct herbicide application to cut stems and hand removal (Table 3.1).

Four floristic measures were used as response variables: Native species richness, exotic species richness, species composition (identity and abundance) and bitou seedling abundance. Exotics were defined as species introduced to the New South Wales coastal zone and included species introduced both from other countries and other

regions of Australia. Bitou seedlings were defined as recently germinated individuals <20 cm tall with limited branching and lignification. Seedlings were counted in a 1m strip at the perimeter of the long axis of each quadrat.

Data analysis

General linear modelling (GLM) (SPSS 2003) was used to determine which physical, disturbance and biotic characteristics predicted native and exotic species richness and bitou seedling abundance in fore dune and hind dune vegetation communities. Data from 0.1 ha quadrats were used. Predictors were removed from the model using a backward elimination process when P values were >0.05 . The non-significant variables are not presented. Data were square root or log transformed when required to conform to assumptions of normality and homogeneity of variance. The Shapiro-Wilk test of normality was used (Miller 1997) and the significance for the test of normality was set at $\alpha = 0.01$ (see Underwood 1997). Multicollinearity was assessed using Pearson and Spearman Correlation Coefficients. Two hind dune and eight fore dune sites were excluded from GLM analyses due to missing values for some independent variables of the model. Exclusion of these sites is unlikely to affect model outcomes as missing values were associated with poor record-keeping of site history which appeared to occur randomly through the dataset. Only the most biologically important interaction terms were included in the models because available degrees of freedom were insufficient for all interaction combinations. Adjusted mean values for species richness and bitou seedling abundance were presented to illustrate the unique effect of a predictor on the dependent variable (refer to Appendix A for unadjusted richness values). Contrast analyses were used to perform focused comparisons between pairs of means. Critical significance levels were adjusted using the Bonferroni approach (Rosenthal & Rosnow 1985).

Species composition in each treatment was examined using univariate and multivariate techniques. A two-way analysis of similarity (ANOSIM) tested the hypothesis that site compositions were similar for different management histories and in northern and southern regions of fore dune and hind dune communities by generating a Bray-Curtis similarity matrix within the PRIMER package (Clarke & Warwick 2001). Species abundance data were square root transformed. Bitou abundance values were excluded from the floristic dataset to examine whether treatment differences were attributable solely to invasion by bitou, or whether other compositional changes were evident. Individual species contributions to within-group similarity and between-group dissimilarity were examined using the similarity percentage (SIMPER) procedure (Clarke & Warwick 2001) and species strongly associated with each invasion category were identified. The significance of individual species responses (based on cover abundance) to bitou invasion and management regimes was then verified using a one-way Analysis of Variance.

Results

I recorded a total of 438 plant species from 101 families during surveys of 99 sites along the New South Wales coastal dune system and I detected 89 exotic species (Appendix B).

Does intensive management in fore dune communities provide better biodiversity outcomes than extensive management?

In fore dune communities, invasion category (Table 3.1) retained explanatory significance in determining native species richness after accounting for other environmental predictors (Table 3.2; Figure 3.3). Non-invaded sites had significantly higher native species richness than all other invasion categories. Intensively managed sites had significantly more native species than extensively managed sites. However, both intensively and extensively managed sites had similar native species richness to the

bitou-invaded sites. In addition, native species richness was correlated positively with log cover and negatively with distance to strandline. Native species richness was also higher in the absence of mining across all bitou cover values (Table 3.2).

Invasion category was also a significant predictor of fore dune exotic species richness (Table 3.2). Intensively managed sites had significantly higher exotic species richness than all other sites (Figure 3.4). Non-invaded, extensively managed and bitou-invaded sites had similar low exotic species richness. Exotic species richness was higher in autumn than summer surveys. At mined sites, exotic species richness was higher where time since fire was recent (<5 yrs). However, at unmined sites, exotic species richness was higher where the fire interval was longer (>5yrs) (Table 3.2).

The most frequently occurring exotic species are listed in Table 3.3. Importantly, bitou was the most frequently encountered exotic species across all sites indicating that while management may reduce bitou cover, neither intensive nor extensive management has succeeded in eradicating this species. In addition, the presence of bitou in 60% of non-invaded sites in fore dune and hind dune communities indicated that non-invaded areas frequently supported bitou at low abundance. The invasives *Asparagus aethiopicus* and *Lantana camara* were relatively frequent in intensively managed fore dune sites (Table 3.3) while incidental exotic species such as *Hydrocotyle bonariensis* and *Solanum nigrum* were frequently encountered in all managed fore dune sites (Table 3.3).

Table 3.2: General linear models for fore dune (n = 57) communities predicting native and exotic species richness using environmental, disturbance and invasion factors and covariates.

Dependent variable	Predictor variable	df	MS	F	P	r^2	Direction of response
Native species richness <i>P</i> < 0.001	Intercept	1	6568.971	283.237	<0.001	0.742	
	INVASION CATEGORY	3	468.645	20.207	<0.001		see Figure 3.3
	BIT_COVER	3	129.861	5.599	0.002		see interaction
	MINING	1	358.291	15.449	<0.001		see interaction
	STRAND	1	347.847	14.998	<0.001		negative correlation
	%LOG	1	173.432	7.478	0.009		positive correlation
	BIT_COVER by MINING	2	88.597	3.820	0.029		while magnitude varied, trend was consistent: higher richness where sand mining was absent across bitou cover values
	Error	45	23.192				
Exotic species richness <i>P</i> < 0.001	Intercept	1	12.845	549.844	<0.001	0.662	
	INVASION CATEGORY	3	0.460	19.674	<0.001		see Figure 3.4
	SEASON	2	0.076	3.232	0.048		summer < autumn
	FIRE	1	1.773×10^{-5}	0.001	0.978		see interaction
	MINING	1	<0.001	0.008	0.931		see interaction
	FIRE by MINING	1	0.121	5.161	0.028		In the absence of mining, richness was higher at sites where time since fire >5 yrs. In the presence of mining, richness was higher at sites where time since fire <5 yrs.
	Error	48	0.023				

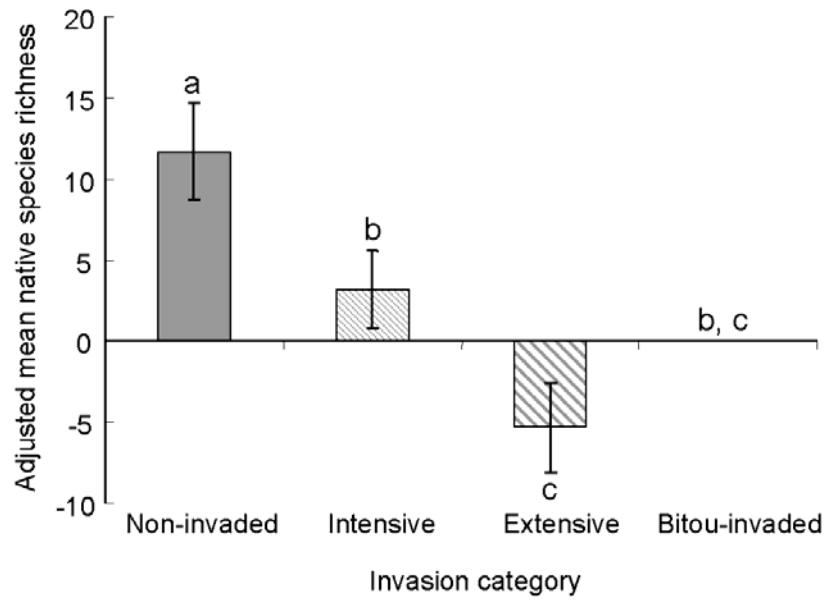


Figure 3.3: Adjusted mean native species richness for each invasion category in fore dune communities (\pm one standard error). Different letters indicate significantly different values (following Bonferroni adjustment).

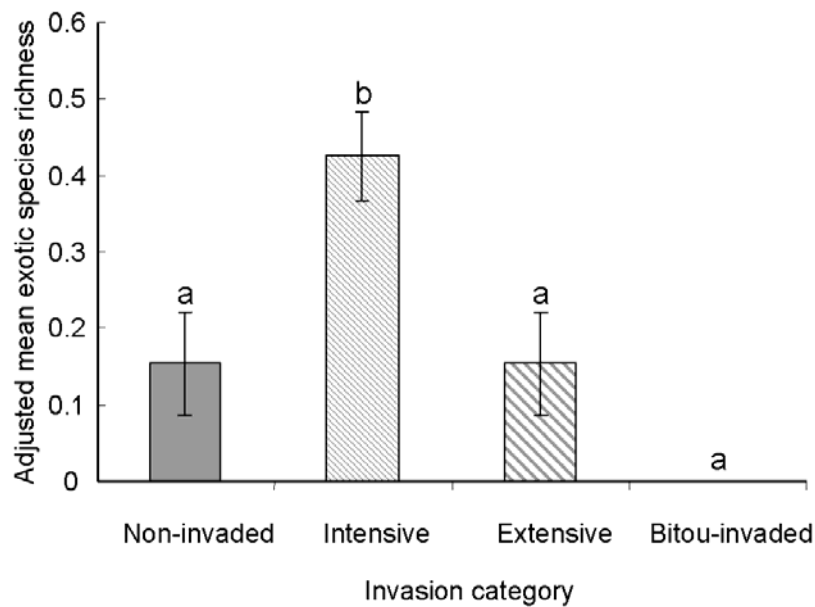


Figure 3.4: Adjusted mean exotic species richness for each invasion category in fore dune communities (\pm one standard error). Different letters indicate significantly different values (following Bonferroni adjustment).

Table 3.3: Exotic species frequency of occurrence (percentage of total quadrats) in fore dune and hind dune communities across invasion categories.

Exotic species	% Frequency			
	Intensively managed	Extensively managed	Non-invaded	Bitou-invaded
Fore dune shrubland				
<i>Chrysanthemoides monilifera</i>	100	85	60	100
<i>ssp. rotundata</i> (bitou)				
<i>Hydrocotyle bonariensis</i>	58	38	-	8
<i>Solanum nigrum</i>	53	38	-	8
<i>Asparagus aethiopicus</i>	42	-	-	-
<i>Lantana camara</i>	26	8	20	50
Hind dune woodland	Managed	Non-invaded	Bitou-invaded	
<i>Chrysanthemoides monilifera</i>	92	60	100	
<i>ssp. rotundata</i> (bitou)				
<i>Conyza sumatrensis</i>	83	-	-	
<i>Asparagus aethiopicus</i>	75	-	-	
<i>Lantana camara</i>	75	-	50	
<i>Solanum nigrum</i>	67	-	-	
<i>Bidens pilosa</i>	58	-	-	
<i>Ochna serrulata</i>	58	-	-	
<i>Senna pendula</i>	50	-	-	
<i>Ehrharta erecta</i>	42	-	-	
<i>Sonchus oleraceus</i>	42	-	-	

In fore dune communities, there were significant species compositional differences between northern and southern sites and between invasion categories (Table 3.4). Pairwise comparisons indicated that all invasion categories were compositionally distinct except for extensively and intensively managed sites (Table 3.4). I then removed all exotic species from the ANOSIM to examine native composition. Similarity between the composition of both intensively managed and non-invaded sites ($R = 0.088$, $P = 0.069$) and intensively managed and bitou-invaded sites ($R = 0.110$, $P = 0.100$) increased when the data were re-analysed using only the native species dataset. However, extensively managed sites remained compositionally distinct from non-invaded sites with removal of exotic species from the analysis ($R = 0.350$, $P = 0.001$) and retained moderate differences with compositions of bitou-invaded sites ($R = 0.147$, $P = 0.059$). Despite low segregation of invasion categories, the species composition

results were similar to species richness results: intensive management improved native species composition outcomes more than extensive management.

Table 3.4: Two-way ANOSIM results from pairwise tests comparing species compositions and abundance across invasion categories in fore dune (n = 65) and hind dune (n = 34) communities (bitou excluded).

Factors	<i>R</i>	<i>P</i>-value
Fore dune		
Site location (north vs. south)	0.378	0.001
Invasion category	0.165	0.001
Pairwise comparisons for invasion category:		
Extensive: Intensive	0.082	0.132
Extensive: Non-invaded	0.317	0.001
Extensive: Bitou-invaded	0.197	0.023
Intensive: Non-invaded	0.108	0.043
Intensive: Bitou-invaded	0.172	0.022
Non-invaded: Bitou-invaded	0.252	0.01
Hind dune		
Site location (north vs. south)	0.300	0.005
Invasion category	0.151	0.021
Pairwise comparisons for invasion category:		
Managed: Non-invaded	0.376	0.002
Managed: Bitou-invaded	0.082	0.142
Non-invaded: Bitou-invaded	0.073	0.187

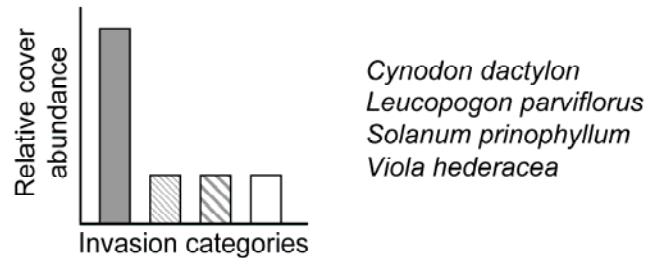
Figure 3.5 models potential responses of fore dune species to bitou invasion and management. Each model is supported by a list of species. These species had consistent responses and were identified using SIMPER analyses. Due to latitudinal variation and small sample sizes for individual species, it was difficult to extract strong indicators. One way ANOVAs were performed on individual species to confirm trends. However, post hoc contrasts were not subjected to Bonferroni adjustment due to low power. Consequently, while a number of analyses point towards patterns in species composition following bitou invasion and management, further targeted sampling is required to consolidate my findings. A number of native species showed reduced abundance following bitou invasion and both intensive and extensive management (Figure 3.5a).

Other native species were poorly represented in extensively managed and bitou-invaded sites only: they were well represented in non-invaded and intensively managed sites (Figure 3.5b). Conversely, the dominant shrubland species *Acacia longifolia* ssp. *sophorae* was less abundant in intensively managed and bitou-invaded sites relative to non-invaded and extensively managed sites (Figure 3.5c). An important native grass coloniser (*Spinifex sericeus*) suffered reduced abundance in bitou-invaded sites, but responded to both intensive and extensive management (Figure 3.5d).

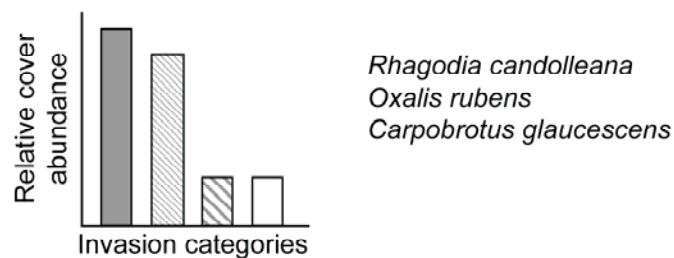
Some response models are not illustrated in Figure 3.5 as they are not depicted by the native dune flora. I could not find any native species which responded more favourably in managed (either intensively or extensively) sites than unmanaged, non-invaded sites (refer to Table 3.3 for exotic species advantaged by management regimes), nor species unaffected by both management and bitou invasion. Finally, I could not find species solely disadvantaged by management regimes and unaffected by bitou invasion, indicating that bitou invasion is a pervasive threat to native species viability.

Model response and example species

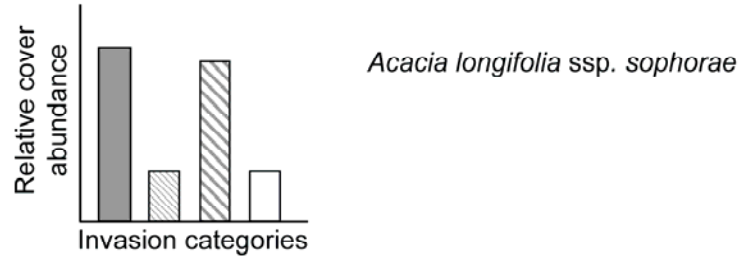
(a) Disadvantaged by bitou invasion and management



(b) Disadvantaged by bitou invasion and extensive management



(c) Disadvantaged by bitou invasion and intensive management



(d) Disadvantaged by bitou invasion

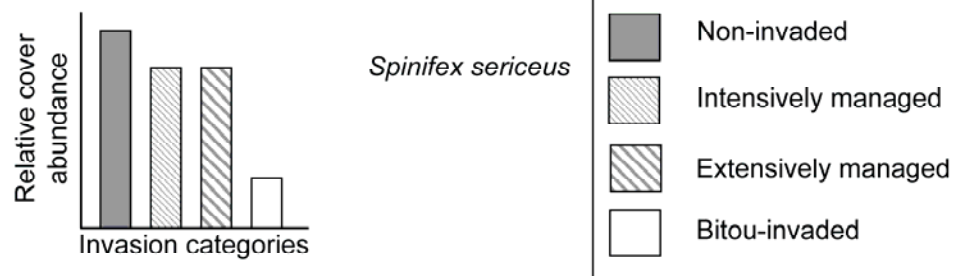


Figure 3.5: Models of fore dune native plant responses to bitou invasion and management and example species which consistently conform to each model in northern and southern sites.

Does management in hind dune communities improve biodiversity outcomes such that managed sites are intermediate between non-invaded and bitou-invaded sites?

In the hind dune model, native species richness was not dependent on invasion category (Table 3.5). Consequently, non-invaded, managed and bitou-invaded sites had similar native species richness (data not shown). Native species richness was negatively correlated with distance from the strandline and cover of standing dead vegetation. Native species richness was also higher where lichen was present, in western rather than eastern sites and on moderately sloped compared with flat sites (Table 3.5). There were also a number of significant two-way interactions between time since fire and sand mining, bitou cover and time since fire and bitou cover and sand mining (Table 3.5). The significant interactions between bitou cover levels and both sand mining presence and time since fire were driven by different magnitudes of response at each bitou cover level rather than different directions of response. Ultimately, sites where sand mining was absent and where time since fire was >5 years supported higher native species richness across all bitou cover values than sites where mining was present and time since fire was <5 years respectively. The significant interaction between sand mining and time since fire was driven by different directions of response: native species richness was higher in recently burned sites (<5 years) where sand mining was absent but where sand mining was present, native species richness was higher in sites with longer fire intervals (>5 years). Interpretation of these interactions must be viewed with caution due to limited replication of sites where both sand mining and recent fire (<5 years) have occurred. Consequently, these significant interactions may indicate future directions for disturbance and invasion ecology research, but are not well explained in the present study.

Invasion category was a significant predictor of hind dune exotic species richness (Table 3.5). Contrast analyses indicated that managed sites had significantly

higher exotic species richness than non-managed bitou-invaded sites. Non-invaded sites had the lowest exotic species richness (Figure 3.6). Exotic species richness was also negatively correlated with log cover and was higher where bryophytes were absent (Table 3.5). There were significant second order interactions between bitou cover and both sand mining and time since fire. The interaction between bitou cover and sand mining was driven by different magnitudes of the effect for sand mining levels at each bitou cover value. However, the presence of sand mining signalled higher exotic species richness across all bitou cover values compared to sites where sand mining was absent. The interaction between bitou cover and time since fire was driven by different directions of the response: at low bitou cover (<5%), exotic species richness was higher when time since fire was >5 years. However, at moderate bitou cover (5-50%), exotic species richness was higher when time since fire was <5 years.

Bitou occurred at high frequency across all hind dune sites (Table 3.3), although abundance was low in non-invaded sites. The incidental exotic *Conyza sumatrensis* contributed markedly to exotic richness values for managed sites. More importantly, frequent occurrence of *Asparagus aethiopicus* and *Lantana camara* in managed hind dune communities signalled potential secondary invasion following bitou removal.

Table 3.5: General linear models for hind dune (n = 32) communities predicting native and exotic species richness using environmental, disturbance and invasion factors and covariates.

Dependent variable	Predictor variable	df	MS	F	P	r ²	Direction of response
Native species richness <i>P</i> = 0.002	Intercept	1	24.465	106.476	<0.001	0.854	
	BIT_COVER	3	2.965	12.905	<0.001		see interaction
	SLOPE	2	0.937	4.080	0.040		trend of 0-5° < 6-10°
	FIRE	1	5.530	24.068	<0.001		see interaction
	MINING	1	5.588	24.321	<0.001		see interaction
	LICHEN	1	3.862	16.808	0.001		absent < present
	LONG	1	4.587	19.963	0.001		negative correlation
	STRAND	1	2.333	10.152	0.007		negative correlation
	% ST_DEAD	1	6.258	27.235	<0.001		negative correlation
	FIRE by MINING	1	6.309	27.458	<0.001		In the absence of mining, richness was higher at sites where time since fire <5 yrs. In the presence of mining, richness was higher at sites where time since fire >5 yrs
	BIT_COVER by MINING	3	1.364	5.938	0.008		while magnitude varied, trend was consistent: higher richness where mining was absent across bitou cover values
	BIT_COVER by FIRE	2	2.468	10.742	0.001		while magnitude varied, trend was consistent: higher richness where time since fire >5 yrs across bitou cover values
	Error	14	0.230				
Exotic species richness <i>P</i> < 0.001	Intercept	1	27.133	445.594	<0.001	0.965	
	INVASION CATEGORY	2	5.643	92.672	<0.001		see Figure 3.6
	BIT_COVER	3	0.348	5.712	0.007		see interaction
	FIRE	1	0.057	0.937	0.347		see interaction
	MINING	1	2.543	41.761	<0.001		see interaction
	BRYOPH	1	0.394	6.470	0.021		absent > present
	% LOG	1	0.576	9.456	0.007		negative correlation
	BIT_COVER by FIRE	2	1.648	27.060	<0.001		at low bitou cover (<5%), richness was higher where time since fire >5 yrs, but at moderate bitou cover (5-50%), richness was higher where time since fire < 5 yrs
	BIT_COVER by MINING	3	0.239	3.923	0.027		while magnitude varied, trend was consistent: higher richness where sand mining was present across bitou cover values
	Error	17	0.061				

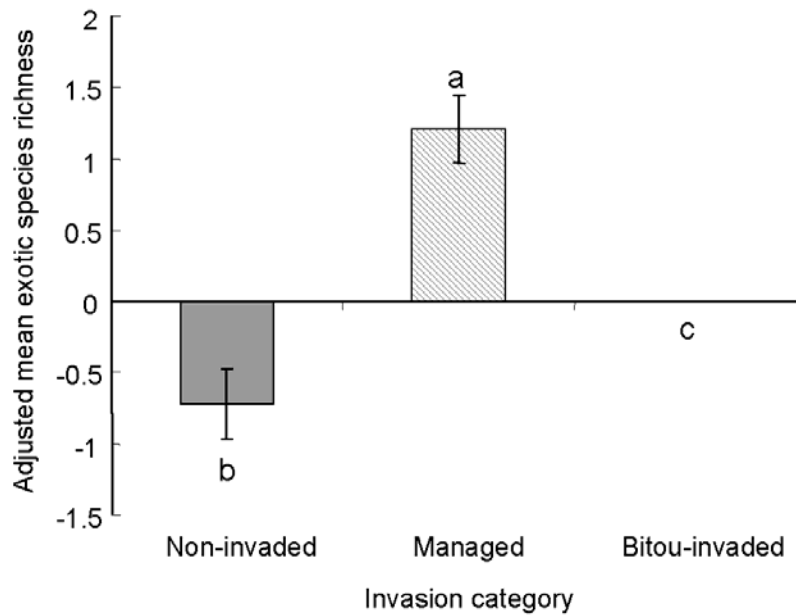


Figure 3.6: Adjusted mean exotic species richness for each invasion category in hind dune communities (\pm one standard error). Different letters indicate significantly different values (following Bonferroni adjustment).

In hind dune communities, there were significant species compositional differences between northern and southern sites and between invasion categories (Table 3.4). Pairwise comparisons indicated that managed sites were compositionally distinct from non-invaded sites but similar to bitou-invaded sites. Bitou-invaded and non-invaded sites were also compositionally similar (Table 3.4). The analysis was rerun with removal of all exotic species to determine whether differences between non-invaded and managed sites were due to exotic compositions alone. While overall differences among invasion categories were marginal ($R = 0.106$, $P = 0.071$), non-invaded and managed native species compositions remained distinct ($R = 0.302$, $P = 0.009$).

Figure 3.7 models hind dune native species responses to bitou management. Bitou-invaded sites were not considered as they were compositionally similar to non-invaded sites (Table 3.4). Species from herb, shrub and tree growth forms had reduced abundance in managed sites compared with non-invaded sites (Figure 3.7a). A

colonising herb and climbers exemplified species which were advantaged by bitou management (Figure 3.7b). Finally, the shrub *Leptospermum laevigatum* appeared unaffected by management regimes (Figure 3.7c).

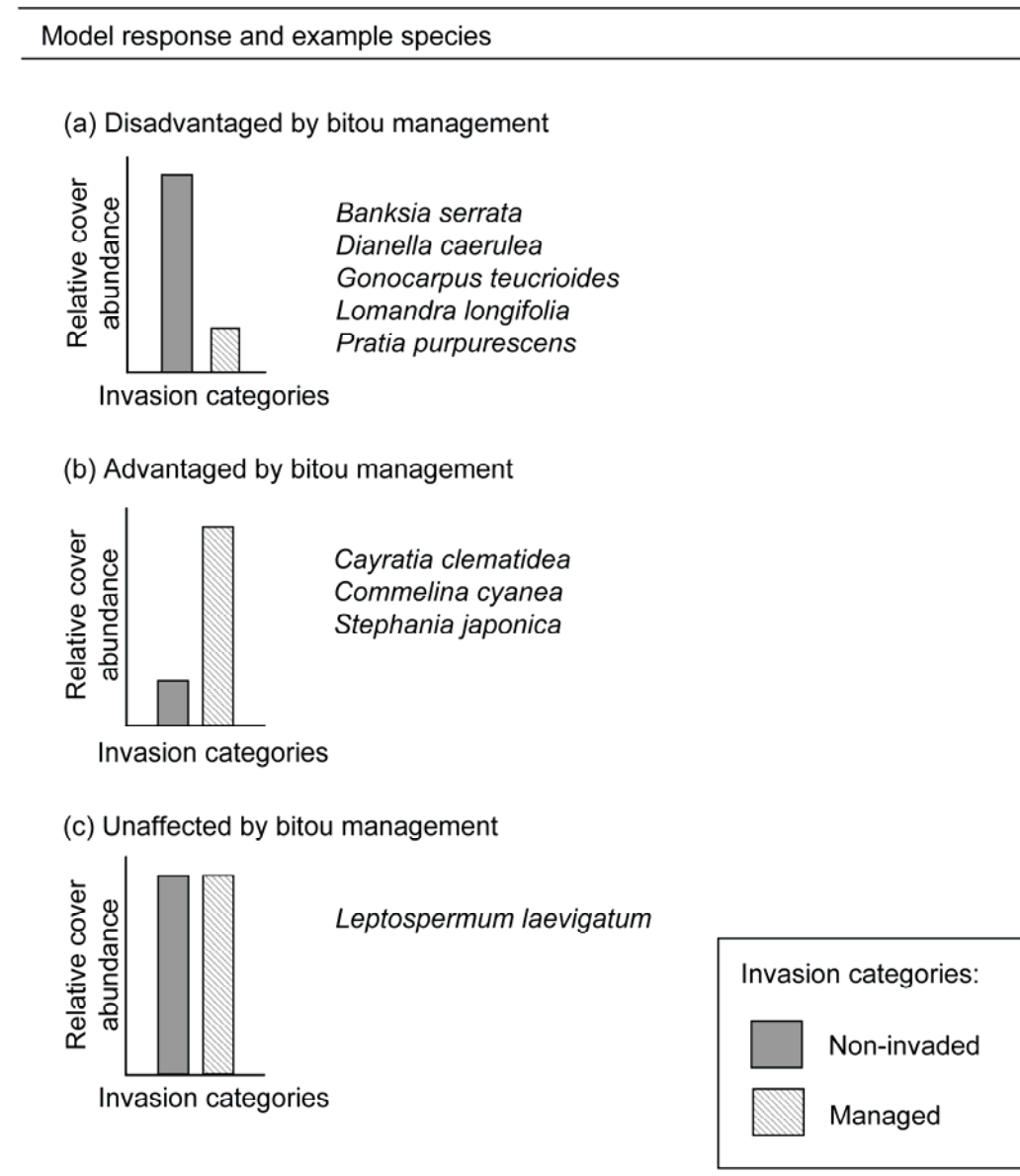


Figure 3.7: Models of hind dune native plant responses to bitou management and example species which consistently conform to each model in northern and southern sites.

Do management activities reduce invader cover and regeneration potential?

All managed sites had lower above-ground bitou percent cover than bitou-invaded sites. This was true for both fore dune (mean \pm standard error: Intensively managed = 16.63 % \pm 5.41; Extensively managed = 9.54 % \pm 3.41; Bitou-invaded = 64.63 % \pm 5.23) and hind dune (mean \pm standard error: Managed = 2.00 % \pm 1.25; Bitou-invaded = 59.42 % \pm 5.04) communities.

I then looked at the response of bitou seedling abundance across sites. In fore dune communities, invasion category was not a significant predictor for bitou seedling abundance. Seedling abundance responded significantly to above-ground bitou cover (0% < 0-5% < 5-50%, 51-100%) (Figure 3.8). In addition, bitou seedling abundance was negatively correlated with litter cover and positively correlated with standing dead vegetation cover (Table 3.6). While different management regimes did not directly affect bitou regeneration, aerial spray programs at extensively managed sites resulted in higher percent standing dead vegetation cover than at intensively managed sites (mean \pm standard error: Extensive: 21.50 % \pm 5.71; Intensive: 6.50 % \pm 1.32). Consequently, bitou regeneration may be higher in extensively than intensively managed fore dune sites due to higher cover of standing dead vegetation.

In hind dune communities, invasion category was not a significant predictor for bitou seedling abundance. However, seedling abundance responded significantly to bitou cover (Table 3.6). Bitou seedling abundance was lowest where bitou cover was absent, but all other bitou cover categories (<5%, 5–50%, 50–100%) yielded similar seedling abundance (Figure 3.9). It appears that bitou regeneration occurs even when above-ground bitou cover is low in both fore and hind dune communities.

Table 3.6: General linear models for fore dune (n = 57) and hind dune (n = 32) communities predicting bitou seedling abundance using environmental, disturbance and invasion factors and covariates.

Vegetation community	Predictor variable	df	MS	F	P	r ²	Direction of response
Fore dune shrubland <i>P</i> < 0.001	Intercept	1	0.673	62.276	<0.001	0.808	
	BIT_COVER	3	0.720	66.641	<0.001		0% < 0-5% < 5-50%, 51-100%
	% ST_DEAD	1	0.127	11.777	0.001		positive correlation
	% LITTER	1	0.119	11.010	0.002		negative correlation
	Error	51	0.011				
Hind dune woodland <i>P</i> < 0.001	Intercept	1	3.329	19.130	<0.001	0.803	
	BIT_COVER	3	1.786	10.261	<0.001		0% < 0-5%, 5-50%, 51-100%
	SEASON	2	1.421	8.166	0.002		spring, summer < autumn
	FIRE	1	3.056	17.564	<0.001		see interaction
	MINING	1	3.000	17.242	<0.001		see interaction
	% LITTER	1	3.182	18.285	<0.001		negative correlation
	% BARE	1	2.264	13.013	0.002		negative correlation
	FIRE by MINING	1	3.013	17.316	<0.001		In the absence of mining, abundance was higher at sites where time since fire <5 yrs. In the presence of mining, abundance was higher at sites where time since fire >5 yrs
	Error	21	0.174				

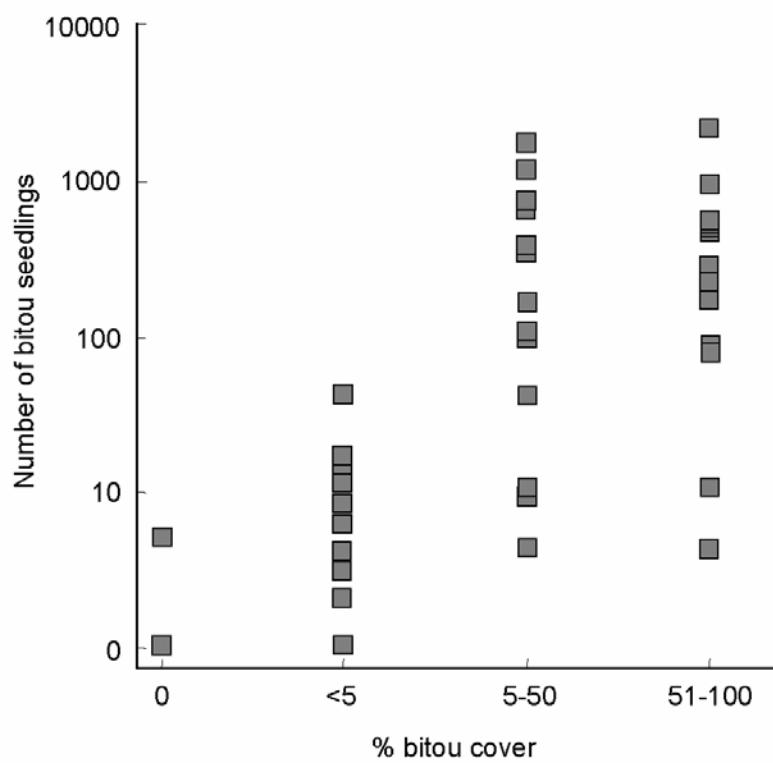


Figure 3.8: Bitou seedling abundance for each cover class (%) of bitou in the standing vegetation in fore dune communities.

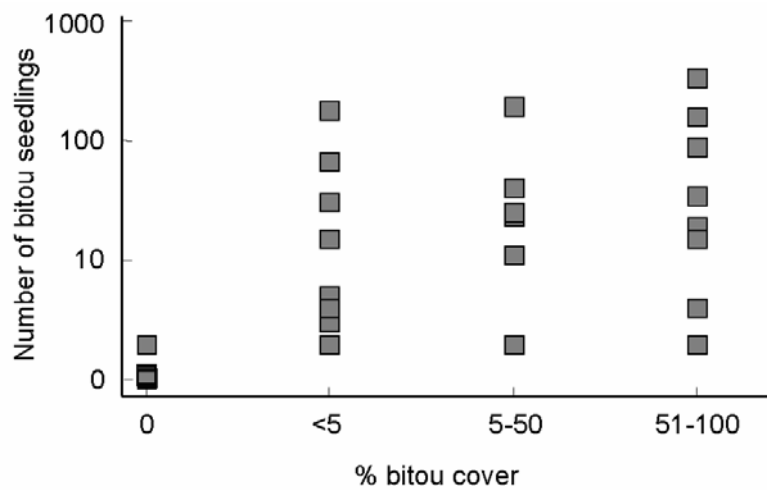


Figure 3.9: Bitou seedling abundance for each cover class (%) of bitou in the standing vegetation in hind dune communities.

Discussion

Management in fore dune communities

Bitou invasion adversely affected fore dune coastal communities with non-invaded sites exhibiting significantly higher native species richness and significantly different species compositions compared with bitou-invaded sites. Plant invasion therefore changed community structure, representing a major disturbance in fore dune communities. While this finding validates management intervention, my results illustrated that control of non-native species is not a restoration panacea. Firstly, the best approach in terms of biodiversity outcomes – intensive management – is expensive and left a residual population of diverse, exotic species which require careful management. Similar proliferation of exotic species has been reported in other systems (e.g. Alvarez & Cushman 2002; Yelenik et al. 2004). Secondly, the cheaper approach of extensive management left depauperate native communities and resulted in high standing dead vegetation cover, in turn increasing light penetration to ground level which may ultimately stimulate bitou regeneration.

Although intensive management delivered better ecological outcomes than extensive management, it was unable to restore native fore dune conditions, supporting fewer native species than non-invaded sites. It is unclear whether management or previous invasion disturbance precipitated native species loss at intensively managed sites. Some herb (*Viola hederacea*, *Oxalis rubens*, *Carpobrotus glaucescens*), grass (*Cynodon dactylon*) and shrub (*Solanum prinophyllum*, *Leucopogon parviflorus*, *Rhagodia candolleana*) species were disadvantaged by both bitou invasion and management. Such species are likely to be poor competitors in bitou-invaded sites and sensitive to herbicide drift or soil disturbance in managed sites. Conversely, the dominant native species *Acacia longifolia* ssp. *sophorae* appeared unaffected by extensive management and non-targeted herbicide application, yet susceptible to

intensive management regimes and bitou invasion, perhaps through trampling or competition following replanting efforts. The colonising grass *Spinifex sericeus*, appeared to respond to management regimes but was adversely affected by bitou invasion, perhaps because bitou stands reduced sand movement and lowered *S. sericeus* germination (see Maze & Whalley 1992a, b).

An important limitation of this observational study was that comparisons across invasion categories may have been confounded by variable site histories which produced different species compositions across categories, thus non-invaded sites may be inherently less invasible than bitou-invaded sites. While I was unable to directly control this issue, comparison of species lists for non-invaded sites in my study with historical data documenting pre- and post-invasion dune vegetation at a lower north coast site (Brewer & Whelan 2003) indicated that species identities were similar between historic pre-invasion and current non-invaded fore dune sites.

Extensive management may exclude native species through the combined effects of bitou invasion and repeated off-target vegetation damage during herbicide application (Wardman & Thomas 2000). Although documented effects of aerial glyphosate application on native coastal species have been negligible (Cooney et al. 1982; Toth et al. 1993), these studies have focused on a limited number of common dune species and have reported short-term findings. In contrast, Matarczyk et al. (2002) found that seedlings and young plants of *Pimelea spicata*, an endangered coastal species, were killed by a single glyphosate application. My findings also suggest that there is a range of species affected by herbicide application. In the long-term, extensive management may fragment large tracts of fore dune communities by excluding native species and disrupting seed dispersal or pollination dynamics. At the landscape scale, species with short-distance dispersal syndromes such as ballistic, gravity or ant-dispersal may have

restricted dispersal potential from proximate non-invaded sites. Extensively managed sites should be interspersed (spatially and temporally) with intensively managed sites and restored with herbicide- or disturbance-sensitive species (refer to Maina & Howe 2000 for related discussion).

My results showed that management itself represents a novel disturbance in invaded fore dune communities with different methodologies invoking different restoration trajectories (cf. Holmes et al. 2000; Antonsen & Olsson 2005). In my system, while neither intensive nor extensive management resulted in dune communities similar to reference native conditions, targeted intensive management maintained a greater diversity of native species than extensive management. Extensively managed sites will require greater intervention through planting or reseedling operations compared with intensively managed sites, to achieve goals of reinstating reference native conditions.

Management in hind dune communities

Hind dune communities responded differently to invasion and management. Here the merits of management were unclear because reference non-invaded and bitou-invaded sites were similar in native species richness and species composition. Consequently, the suite of species characterising non-invaded sites was retained following bitou invasion, despite considerable bitou cover (average of 60%). Greater structural complexity of hind dune woodlands compared with fore dune shrublands may result in asymmetric competition for light resources and, under such conditions, founder effects may control the degree of invasion and result in species coexistence (Rees & Bergelson 1997; Perry et al. 2003). Consequently, at present, impacts of bitou invasion are unclear in hind dune communities. In contrast, management represented a significant disturbance in the hind dune. A number of native herb (*Dianella caerulea*,

Lomandra longifolia and *Pratia purpurescens*) and a low shrub (*Gonocarpus teucroides*) species were disadvantaged by bitou management.

In hind dune communities, invasion did not affect biodiversity values; however managed sites had higher exotic species richness and different native species compositions to non-invaded sites indicating that management has not reinstated native conditions. While initial assessment highlights adverse impacts of management, I do not advocate cessation for three reasons: (1) restoration potential of bitou-invaded hind dune communities is high with retention of the suite of native species characterising non-invaded sites, (2) management may mitigate against senescence of existing native individuals and dispersal limitation which may occur with on-going bitou invasion and (3) management reduces bitou biomass which may limit future invasion potential of both hind and fore dune communities.

Bitou seedling regeneration

Bitou seedling abundance in both fore and hind dune communities did not differ across invasion categories indicating that management has not suppressed bitou regeneration. However, cover of adult bitou individuals was a significant predictor in hind dune and fore dune communities alike. While this result was expected, I found, particularly in the hind dune, that where bitou cover was absent, seedling abundance was low, but at all other cover classes, seedling abundance was similar. Consequently managers must continue to control bitou regeneration (from both the seed rain and seed bank) even when bitou cover is low in the standing vegetation.

In both fore and hind dune communities, litter cover had a suppressive effect on bitou seedling abundance. Similar litter effects have been reported elsewhere (Facelli, 1994; Foster and Gross 1998). Fore dune communities also had increased bitou seedling abundance at sites with high standing dead vegetation cover. I infer that bitou

germination and seedling growth are more successful under standing dead than foliated vegetation due to increased light intensity at the ground layer. Such a finding has important management implications: aerial spraying associated with extensive management creates open patches underneath dead vegetation (T. Mason pers. obs.) which may stimulate further bitou regeneration.

Management and secondary invaders

Intensively managed fore dune and managed hind dune sites supported significantly higher exotic species richness and had higher and more frequent localised disturbance levels compared with all other invasion categories. Intensive management of bitou may release resources such as light or nutrients that other exotic species may then sequester (see Davis et al. 2000). Furthermore, soil disturbance provides colonisation opportunities and reduces neighbour shoot and root competition (McIntyre et al. 1995). In addition, release and dispersal of some seeds have been demonstrated to increase following trampling disturbance (Bertiller 1996). Extensively managed fore dune sites supported significantly fewer exotic species than intensively managed sites. Remote management via aerial spraying may have resulted in fewer, less frequent disturbances (such as trampling) at these sites. Alternatively, propagule pressure may be higher in intensively managed sites with workers importing non-native seed on tools or clothing. Bitou-invaded fore dune sites also had low exotic species richness, suggesting that bitou out competes or inhibits germination of both native and exotic species. My findings therefore do not follow an “invasional meltdown” model (Simberloff & Von Holle 1999) where one invader facilitates invasion by additional species. Bitou may create a stable, undisturbed microenvironment which resists further invasion.

Conclusion

My findings clearly demonstrated that both the invasion process and management activities affected native fore dune community dynamics, while management activities alone affected hind dune community dynamics. While invaders are known to change community dynamics, impacts of management regimes are rarely evaluated, limiting our understanding of conservation outcomes. This study found that all investigated management regimes had adverse impacts on species richness or composition thus management regimes must be considered a form of disturbance by conservation managers. However, intensive management of fore dune sites provided better biodiversity outcomes in terms of native species richness and composition when compared with extensive management. This study focused on ecological outcomes of management techniques; however, I acknowledge that financial constraints of labour-intensive methods limit their application across the landscape. Intensive management of bitou-invaded sites should be prioritised in high conservation communities. Where intensive management is prohibitively expensive, managers must consider the conservation benefit of reduced bitou biomass and likelihood of spread against reduced native species richness and changed species composition following extensive management. Managers may either direct control efforts elsewhere or supplement extensive management with reseedling or replanting of affected native species or growth forms.

In both fore and hind dune communities, follow up activities will be required to eliminate bitou regeneration, avoid secondary invasion and replace native species adversely affected by bitou invasion and management techniques. Follow up activities may become less frequent or intensive as invader seed banks are exhausted. Seed banks may be reduced both by natural attrition and biocontrol activity. A number of biocontrol agents have been released in New South Wales to target bitou seed production and

viability, however the success of release programs in reducing seed production has been variable (refer to Holtkamp 2002, Stuart et al. 2002). Evaluation of biocontrol efficacy in reducing bitou seed banks and assisting follow up activities is now required.

This study highlights a number of detrimental non-target effects following practical invader control. Such effects are evident under different management regimes and must be considered in the design of any invader control program which prioritises biodiversity conservation. Ecological assessment of invader control programs is essential in achieving adaptive management.

Chapter 4

Impacts of a woody invader vary in different resident vegetation communities

Introduction

Plant invasion is a major cause of change in native communities around the world. Plant invaders have been documented as novel dominants (Ortega and Pearson 2005), ecosystem changers (Vitousek 1990; Evans et al. 2001) and agents of biodiversity decline (Enserink 1999; McKinney and Lockwood 1999). In light of profound ecological changes caused by the invasion process, considerable theoretical and experimental work has been conducted to understand invasion mechanisms, predict potential invaders and characterise invaded communities. Numerous plant traits which assist in competitive or coloniser superiority have been recognised in plant invaders (Baker 1965; Bazzaz 1986; Pywell et al. 2003). Invader success may also depend on environmental attributes. Disturbance and invasion success have been positively correlated in a number of studies (Hobbs and Huenneke 1992; D'Antonio 1993; Burke and Grime 1996). External inputs of resources or their release by the resident community (through plant mortality or damage) following disturbance events may provide invasion opportunities (Davis et al. 2000). Consequently the mechanisms by which a species invades and its effects may relate to attributes of the invader, or environmental conditions of the invaded community (Bazzaz 1986), or to a combination of invader and environmental attributes (Didham et al. 2005).

While both invader attributes and community invasibility have been researched, the effects of a single invader on components of different resident communities have rarely been reported (but see D'Antonio et al. 2000). Here I use comparative data to

examine impacts of a single invader in two coastal vegetation communities. I focus on bitou bush *Chrysanthemoides monilifera* ssp. *rotundata* (D.C.) Norl. (hereafter termed bitou), a South African shrub, which has invaded both fore dune shrublands and hind dune woodland / forest communities on the east coast of Australia.

Invasion impacts on native growth forms

Bitou may achieve dominance in dune communities by competitively displacing subordinates by resource consumption: the invader population size increases until the limiting resource is at such a low level that subordinates are unable to survive (Tilman 1988). Consequently, bitou may competitively exclude other shrub species which use similar resources (MacArthur 1972; Johansson and Keddy 1991). Bitou may also competitively exclude functionally dissimilar low architecture herb and graminoid species by reducing light penetration to lower strata. Such exclusion of herbaceous species following woody invasion has previously been documented (e.g. Hobbs and Mooney 1986; Wearne and Morgan 2004). Bitou may also become abundant at a site through tolerance of non-competitive processes such as novel disturbance and an ability to overcome recruitment limitation. These processes may limit the distribution of other species more than the invader (Seabloom et al. 2003b; MacDougall and Turkington 2005).

Bitou has invaded two vegetation communities (fore dune shrubland and hind dune woodland / forest communities) which are distinct in terms of vegetation structure, composition and disturbance history. The fore dune environment is affected both by natural disturbance regimes such as wind and storm action (Viles and Spencer 1995), and anthropogenic disturbance such as sand mining or recreational activities (Chapman 1989; Brown and McLachlan 2002). The hind dune environment is buffered from much of the natural and human-induced disturbance experienced on fore dunes. The hind dune

also has greater structural complexity than the fore dune: hind dune communities have tall shrub and canopy strata while fore dune communities have only a shrub layer with some isolated emergents. Vegetation composition and structure, coupled with disturbance history may moderate bitou impacts in different communities. I hypothesised that native species would be affected by invasion, but the response of different growth forms in each community was unclear.

Invasion impacts on vegetation structure

Invaders continue to interact with the resident community subsequent to the initial invasion. Over time, an invader shifts the proportion of biomass of each species in the assemblage (Johnston 1986). Changes in representation of growth forms may then be expressed in the distribution of vegetation structure. I hypothesised that structural density in both fore and hind dune invaded communities would be re-distributed such that shrub-level vegetation density – corresponding with bitou biomass – would be higher than in non-invaded communities. Structural density at other vegetation heights may be unchanged or reduced following invasion: fore and hind dune ground level structure may be sparser, yet hind dune canopy level structure may be unchanged in bitou-invaded compared with non-invaded communities. Therefore at the community level, the invasion process creates a biotic filter, selectively reducing or eliminating particular morphologies and ultimately changing community structure.

Invasion impacts on community variability

While I have described invasion mechanisms and impacts that may operate at the site level, species exclusion or reduced abundances following invasion may result in changes to community variability at larger spatial scales. Site-to-site variability may increase, decrease or remain the same following invasion. The invasion literature has viewed invaders as homogenizing regional and biome-level floras (McKinney and

Lockwood 1999), but there is little empirical evidence for changed species variability at the community level. If invasion is considered a disturbance (Lockwood et al. 2005), there is little consensus in the literature on the impacts of disturbance on community variability. For example in marine systems, increased (Warwick and Clarke 1993), unchanged and reduced (Chapman et al. 1995; Stark et al. 2003) assemblage variability following disturbance have been reported.

Changes in community variability will depend on the composition of species affected by the invader. I hypothesised that site variability would increase following invasion if widespread or dominant species were lost from communities. This would leave each site with rarer or more restricted species and therefore increase the dissimilarity of bitou-invaded sites. In contrast, I hypothesised that site variability would decrease following invasion if rare or restricted species were lost from communities. Common species which were retained would increase homogeneity across bitou-invaded sites. Unchanged variability following invasion may indicate either a lack of invader impacts or a loss across sites of both widespread and restricted or rare species. According to my hypotheses, a change in variability of community assemblage following invasion would indicate that species representations have become discontinuous at regional scales. Reducing the size and increasing the isolation of populations may increase their extinction risk due to inbreeding depression and stochastic events (van Groenendael et al. 1998; Lennartsson 2002). Local extinction of native species, expressed through changed community variability may then compound impacts of the original invasion.

In this study, my objective was to examine impacts of bitou invasion in two different coastal vegetation communities by comparing species richness of growth

forms, vegetation structural density and site-to-site variability in species composition between bitou-invaded and non-invaded sites.

Methods

Study area

Dune communities were sampled along approximately 1 330 km of the New South Wales (NSW) coast (28° 25' 45" S; 153° 33' 25" E to 36° 57' 37" S; 149° 56' 07" E). Fore dune sites were predominantly *Acacia longifolia* ssp. *sophorae* shrubland with occasional *Banksia integrifolia* emergents. Mid and lower strata species commonly included *Scaevola calandulacea*, *Lomandra longifolia* and *Spinifex sericeus*. Hind dune sites were woodland or forest communities. *Eucalyptus pilularis* and *Banksia integrifolia* were common canopy species. Mid stratum dominants included *Monotoca elliptica* and *Banksia serrata*, while lower stratum species included *Lomandra longifolia* and *Pteridium esculentum*. I defined non-invaded sites as those with little bitou cover (average of 5 %) and no history of invader control activities (fore dune: n = 17; hind dune: n = 10). These sites were the best representatives of relatively undisturbed coastal communities. I defined bitou-invaded sites as having high bitou cover (average of 60 %) and no history of control activities (fore dune: n = 16; hind dune: n = 12). Non-invaded and bitou-invaded sites were interspersed along the coast. Site history was ascertained from (1) responses to a land manager survey, which was distributed to public agency and community group representatives, (2) site records and (3) personal observations (T.J. Mason).

Field methods

Sampling was conducted between September 2002 and May 2003. At each site, a 20 x 50 m (0.1 ha) quadrat was used to measure species identity, vegetation structure and environmental variables. A nested 20 x 20 m quadrat was used to record cover of

each species using an adapted Braun-Blanquet cover scale measure (Poore 1955). The analysis used cover class midpoints. I measured environmental variables of standing dead vegetation, litter, bare ground and log (bole diameter > 0.1 m) percent cover, slope, aspect, distance to strandline and evidence of sand mining or recent fire (< 5 years). These physiogeographic and disturbance variables were measured to account for extrinsic factors that may co vary with diversity of native and invading species in dune communities. Vegetation structure was estimated using an adapted point intercept method (Mueller-Dombois and Ellenberg 1974; Chalmers and Parker 1986). A 16 mm diameter, 3 m wooden pole was divided into 7 height classes (0-0.2m; 0.2-0.5m and thereafter 0.5m increments to 3m). Fifty measurements were taken at 5 pace intervals around the perimeter and down the long axis centreline of the 20 x 50 m quadrat. At each position, the presence or absence of vegetation touching the pole at each height class was recorded. For the purposes of this study, vegetation >3 m tall was considered canopy cover and was estimated at the same interval as understorey structure using a modified moosehorn crown closure estimator (Mueller-Dombois and Ellenberg 1974).

Data analysis

A general linear modelling (GLM) approach was used to assess the impact of bitou invasion on the species richness of native communities. Extrinsic physical, disturbance and biotic predictors were also included in models. Response variables were separated into native and exotic graminoid, herb, shrub, tree and climber species richness at each fore and hind dune site. I used growth forms to express gross differences in plant architecture and functionality (Johnston 1986; Troumbis and Memtsas 2000). Native or exotic status for each species was recorded. Species information was obtained from the NSW plant database (Plant Information Network System of the Botanic Gardens Trust Version 2.0: <http://plantnet.rbgsyd.nsw.gov.au/>).

Exotics were defined as species introduced to the NSW coastal zone, and included species such as *Acacia saligna* which has been introduced from Western Australia.

Predictors were removed from each model using a backward elimination process when P values were >0.05 . Non-significant variables are not presented. Data were transformed to reduce heteroscedasticity and improve normality when required. Multicollinearity was checked using Pearson and Spearman Correlation Coefficients. A number of variables were omitted due to high correlation: bitou cover was removed from fore and hind dune models, while longitudinal position and litter cover were omitted from hind dune models. Complete interaction terms could not be included due to limited available degrees of freedom. For clarity, unadjusted mean richness values of growth forms are graphically presented (trends are the same as adjusted mean value results).

One-way analysis of similarity (ANOSIM) was used to compare vegetation structure between non-invaded and bitou-invaded sites in fore or hind dune communities (Clarke and Warwick 2001). Bitou bush was included in the analysis and the Bray-Curtis similarity index was used on untransformed data. T-tests were then used to determine whether vegetation structure classes were significantly different between non-invaded and bitou-invaded sites.

Variability among species assemblages of non-invaded and bitou-invaded sites was compared using a Permutational Test of Multivariate Dispersion (PERMDISP) (Anderson 2004). The program investigates variability in sets of sites in multidimensional space by calculating (using a similarity index) how distant each site is from an average site (centroid). In my case, dimensions were associated with species identity and cover abundance. PERMDISP then tests whether variability in two sets of sites (non-invaded and bitou-invaded) differs through a randomisation permutation

procedure. The test requires a balanced design so one non-invaded fore dune and two bitou-invaded hind dune sites were omitted from each one way analysis (fore dune: $n = 16$; hind dune: $n = 10$). Tests used Bray-Curtis dissimilarities with 9999 permutations on unstandardised data. Non metric multidimensional scaling (nMDS) was used to illustrate spatial patterns (Field et al. 1982). I used untransformed, square root transformed, fourth root transformed and presence-absence data to progressively down-weight the effects of abundant species and increase the importance of rare species. I omitted bitou cover abundance values to analyse invader effects on the remainder of the dune community. I used the SIMPER procedure (Clarke and Warwick 2001) to select species with high contributions to invasion category dissimilarities.

Results

Growth form responses

In fore dune communities, non-invaded sites had significantly more native graminoid, herb and climber species than bitou-invaded sites (Table 4.1; Figure 4.1a-c). In contrast, invasion category explained little variation in native shrub and tree richness and was not retained in the final model (Table 4.1). Exotic herb richness was higher in non-invaded compared with bitou-invaded sites (Table 4.1; Figure 4.1d) but invasion category was not a significant predictor for exotic graminoid and climber species richness (Table 4.1). As there were only two records of exotic trees in fore dune communities (*Acacia saligna* and *Coprosma repens*), this growth form was not analysed. When bitou was excluded from the analysis, exotic shrubs did not respond significantly to invasion category. It should be noted that the final exotic shrub model was non normal and heterogeneous indicating the significance of factors remaining in the model may be equivocal. However, as invasion category was non significant in the

final model, the central finding that native and exotic shrub species responded similarly to bitou invasion was unaffected.

A number of disturbance and environmental predictors remained significant in final fore dune models (Table 4.1). Shrub species richness was reduced in sand mined sites. Aspect, latitudinal position and distance to strandline were significant environmental predictors but trends were not consistent across growth forms. Litter cover was positively correlated with native shrub richness, while log cover was negatively correlated with exotic graminoid richness. Native herb and exotic graminoid richness values were higher in western than eastern sites in the study area.

In hind dune communities, non-invaded sites had significantly more native shrub species than bitou-invaded sites (Table 4.2; Figure 4.1e). Native shrub species richness was negatively correlated with distance to strandline and cover of standing dead vegetation, but positively correlated with cover of bare ground. Native shrub species richness was also reduced at sand mined sites. The native graminoid, herb, tree and climber species richness models were non significant (Table 4.2), indicating that recognised factors and covariates were unable to explain hind dune richness for these growth forms. Similarly, invasion category was not a significant factor predicting exotic graminoid, herb, shrub and climber richness in hind dune communities (Table 4.2). As the study did not record any exotic tree species in the hind dune, tree growth form responses were not analysed. Exotic shrub richness was higher in areas that were sand mined and in northern sections of the study area, but richness was not related to invasion category (Table 4.2).

Table 4.1: General linear models for fore dune (n = 32) communities predicting species richness of growth form groups using environmental and disturbance factors and covariates.

Growth form species richness	Model <i>P</i>	<i>r</i> ²	Predictor variable	df	MS	F	<i>P</i>	Direction of response
Native graminoid	0.0001	0.366	Intercept	1	699.427	158.012	0.0001	see Figure 4.1(a)
			Invasion category	1	76.677	17.323	0.0001	
			Error	30	4.426			
Native herb	0.0001	0.742	Intercept	1	74.973	16.719	0.0001	see Figure 4.1(b) NE-SE > NW-SW, SE-SW negative correlation
			Invasion category	1	137.848	30.741	0.0001	
			Aspect	3	26.453	6.392	0.002	
			Longitudinal position	1	20.805	4.640	0.041	
			Error	26	4.484			
Native shrub	0.001	0.527	Intercept	1	0.502	0.180	0.674	SE-SW highest absent > present positive correlation
			Aspect	3	12.933	4.647	0.01	
			Sand mining	1	54.727	19.662	0.0001	
			Litter	1	18.352	6.594	0.016	
			Error	26	2.783			
Native tree	0.461		Model non significant					
Native climber	0.001	0.382	Intercept	1	42.040	13.007	0.001	see Figure 4.1(c) positive correlation
			Invasion category	1	29.885	9.247	0.005	
			Latitudinal position	1	49.769	15.398	0.0001	
			Error	29	3.232			
Exotic graminoid	0.003	0.330	Intercept	1	4.631	77.509	0.0001	negative correlation negative correlation
			Longitudinal position	1	0.823	13.779	0.001	
			Log	1	0.286	4.793	0.037	
			Error	29	0.060			
Exotic herb	0.0001	0.742	Intercept	1	0.383	15.057	0.001	see Figure 4.1(d) negative correlation positive correlation
			Invasion category	1	0.701	27.543	0.0001	
			Latitudinal position	1	0.301	11.842	0.002	
			Distance to strandline	1	0.142	5.567	0.026	
			Error	28	0.025			
Exotic shrub	0.022	0.232	Intercept	1	0.306	8.709	0.006	absent > present negative correlation
			Sand mining	1	0.199	5.677	0.024	
			Distance to strandline	1	0.194	5.522	0.026	
			Error	29	0.035			
Exotic climber	0.056		Model non significant					

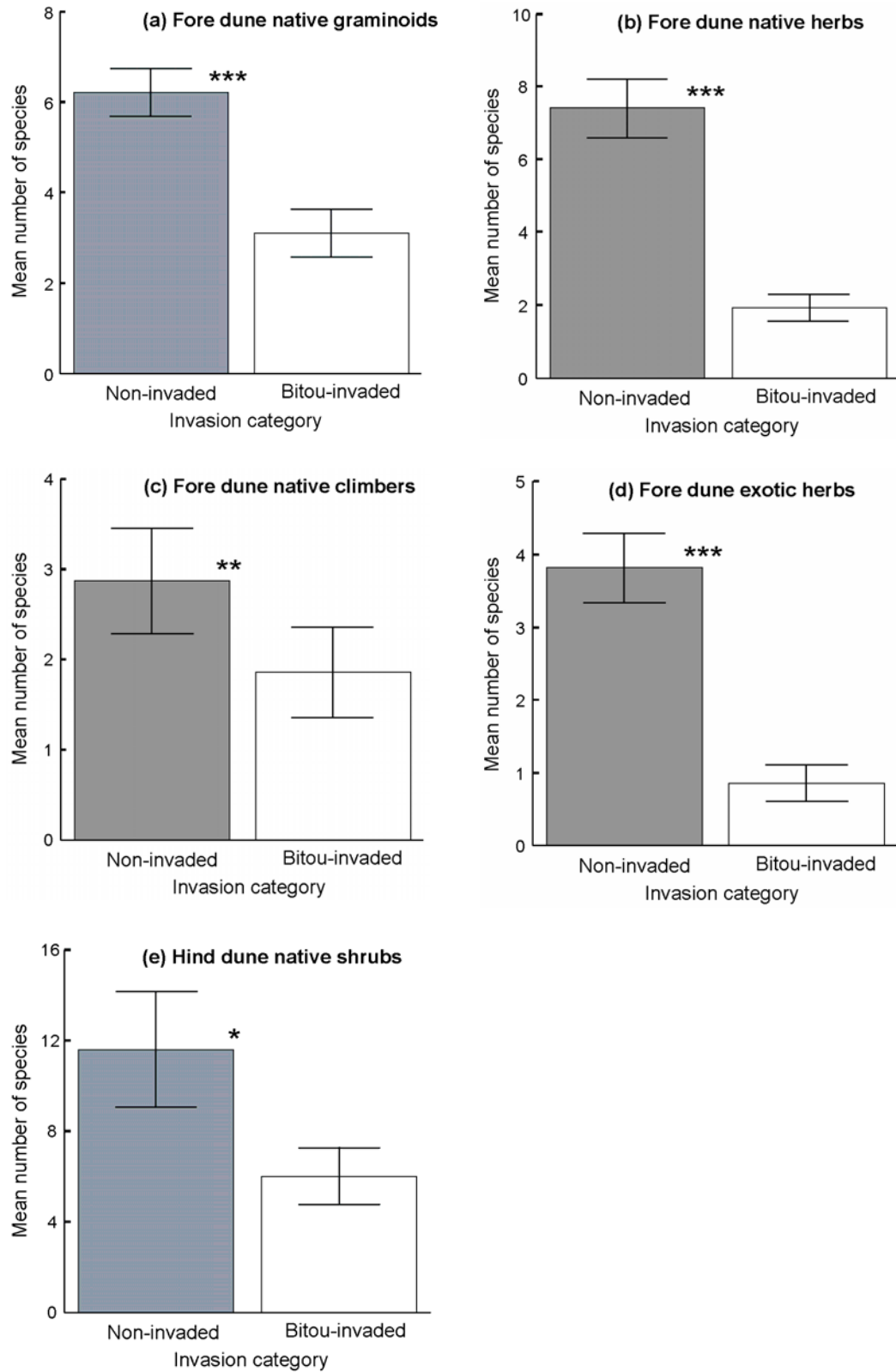


Figure 4.1: Mean species richness of different growth forms for non-invaded and bitou-invaded fore dune and hind dune sites (\pm one standard error) * $P < 0.05$; ** $P < 0.01$; * $P < 0.001$.**

Table 4.2: General linear models for hind dune (n =22) communities predicting species richness of growth form groups using environmental and disturbance factors and covariates.

Growth form species richness	Model <i>P</i>	<i>r</i> ²	Predictor variable	df	MS	F	<i>P</i>	Direction of response
Native shrub	0.001	0.811	Intercept	1	487.639	35.184	0.0001	
			Invasion category	1	79.726	5.752	0.032	see Figure 4.1(e)
			Aspect	3	126.656	9.138	0.002	NE-NW > NE-SE, NW-SW and SE-SW > NW-SW
			Sand mining	1	65.894	4.754	0.048	absent > present
			Distance to strandline	1	95.146	6.865	0.021	negative correlation
			% Bare ground	1	83.079	5.994	0.029	positive correlation
			% Standing dead vegetation	1	93.489	6.745	0.022	negative correlation
			Error	13	13.860			
Exotic shrub	0.002	0.489	Intercept	1	0.123	1.894	0.185	
			Sand mining	1	0.367	5.662	0.028	absent < present
			Latitudinal position	1	0.326	5.039	0.037	positive correlation
			Error	19	0.065			
Native graminoid	0.085		Model non significant					
Native herb	0.184		Model non significant					
Native tree	0.119		Model non significant					
Native climber	0.095		Model non significant					
Exotic graminoid	0.181		Model non significant					
Exotic herb	0.155		Model non significant					
Exotic climber	0.281		Model non significant					

Vegetation structure

Vegetation structure was significantly different in bitou-invaded and non-invaded sites in both fore and hind dune communities (Table 4.3). In fore dune communities, bitou-invaded sites were characterised by a denser shrub layer (0.2-1 m) and sparser ground cover layer (0-0.2m) than reference non-invaded sites (Table 4.3). In hind dune communities, structural differences consisted of greater understorey density (0.2-1.5 m) but reduced canopy density (>3 m) in bitou-invaded sites compared with non-invaded sites (Table 4.3).

Table 4.3: One-way analysis of similarities (ANOSIM) test and post hoc t-test results for vegetation structure of non-invaded and bitou-invaded sites in fore dune and hind dune communities (untransformed data).

Community	ANOSIM results		t-test results		
	R Statistic	P value	Height categories	P value	Bitou-invaded vs. Non-invaded*
Fore dune	0.143	0.012	0-0.2 m	0.043	B < N
			0.2-0.5 m	0.001	B > N
			0.5-1.0 m	0.006	B > N
			1.0-1.5 m	0.128	B = N
			1.5-2.0 m	0.626	B = N
			2.0-2.5 m	0.887	B = N
			2.5-3.0 m	0.578	B = N
			> 3.0 m	0.545	B = N
Hind dune	0.246	0.003	0-0.2 m	0.375	B = N
			0.2-0.5 m	0.027	B > N
			0.5-1.0 m	0.004	B > N
			1.0-1.5 m	0.003	B > N
			1.5-2.0 m	0.869	B = N
			2.0-2.5 m	0.205	B = N
			2.5-3.0 m	0.131	B = N
			> 3.0 m	0.007	B < N

* B = Bitou-invaded sites; N = Non-invaded sites

Community variability

In fore dune communities, bitou-invaded sites were significantly more variable than non-invaded sites when species cover abundances were considered (Table 4.4). Stress levels for the nMDS plot were high (Figure 4.2a-c), indicating that sites were not well represented in two dimensions, but formal PERMDISP analyses confirmed the plot trends. Native species with strong contributions to dissimilarities between site categories had lower cover in bitou-invaded sites than in non-invaded sites (Table 4.5). These species also occurred less frequently in bitou-invaded than non-invaded sites, but *Acacia longifolia* ssp. *sophorae*, *Banksia integrifolia*, *Leptospermum laevigatum* and *Hibbertia scandens* had similar frequencies in non-invaded and bitou-invaded sites (Table 4.5). However, when species richness (i.e., presence / absence) data were considered, there was similar variability between fore dune non-invaded and bitou-invaded sites (Table 4.4; Figure 4.2d), suggesting that changes in species cover, rather than richness or identity, was the primary driver of increased fore dune variability following bitou invasion.

In hind dune communities, non-invaded and bitou-invaded sites had similar community variability regardless of species cover weightings (i.e., untransformed, square root and fourth root transformed or presence / absence data) (Table 4.4; Figure 4.2e-h). This result indicated that either bitou invasion did not affect overall cover of species and their identity, or that widespread and restricted / rare species were affected by invasion. I previously found that overall native species richness and composition were similar among hind dune non-invaded and bitou-invaded sites (Chapter 3), so I discounted the second possibility and concluded that bitou invasion had not affected hind dune community variability.

Table 4.4: Permutational analysis of multivariate dispersions (PERMDISP) for fore and hind dune communities under various transformations (analyses exclude bitou abundances).

Transformation sequence:	Untransformed (raw abundances)	Square root ($\sqrt{}$)	Fourth root ($\sqrt[4]{}$)	Presence /Absence
Transformation explanation:	Weighted for abundant species	\longrightarrow		Equal weighting for all species
Fore dune	N<B *	N<B *	N<B *	ns
Hind dune	ns	ns	ns	ns

* $P < 0.05$; ns = non significant N = Non-invaded sites; B = Bitou-invaded sites.

Table 4.5: SIMPER results and associated abundance and frequency information for native species with the highest contribution to dissimilarities between non-invaded and bitou-invaded fore dune sites.

Species	Average abundance (% cover)		Frequency (%)	
	Non-invaded	Bitou-invaded	Non-invaded	Bitou-invaded
<i>Acacia longifolia</i> ssp. <i>sophorae</i>	24.81	13.25	100	88
<i>Banksia integrifolia</i>	7.19	7.00	82	81
<i>Leptospermum laevigatum</i>	6.88	1.88	41	38
<i>Spinifex sericeus</i>	6.19	1.00	100	63
<i>Lomandra longifolia</i>	5.63	1.38	76	38
<i>Leucopogon parviflorus</i>	5.31	2.69	94	69
<i>Hibbertia scandens</i>	2.75	0.81	53	50
<i>Carpobrotus glaucescens</i>	1.88	1.00	94	50
<i>Isolepis nodosa</i>	1.88	1.06	82	56

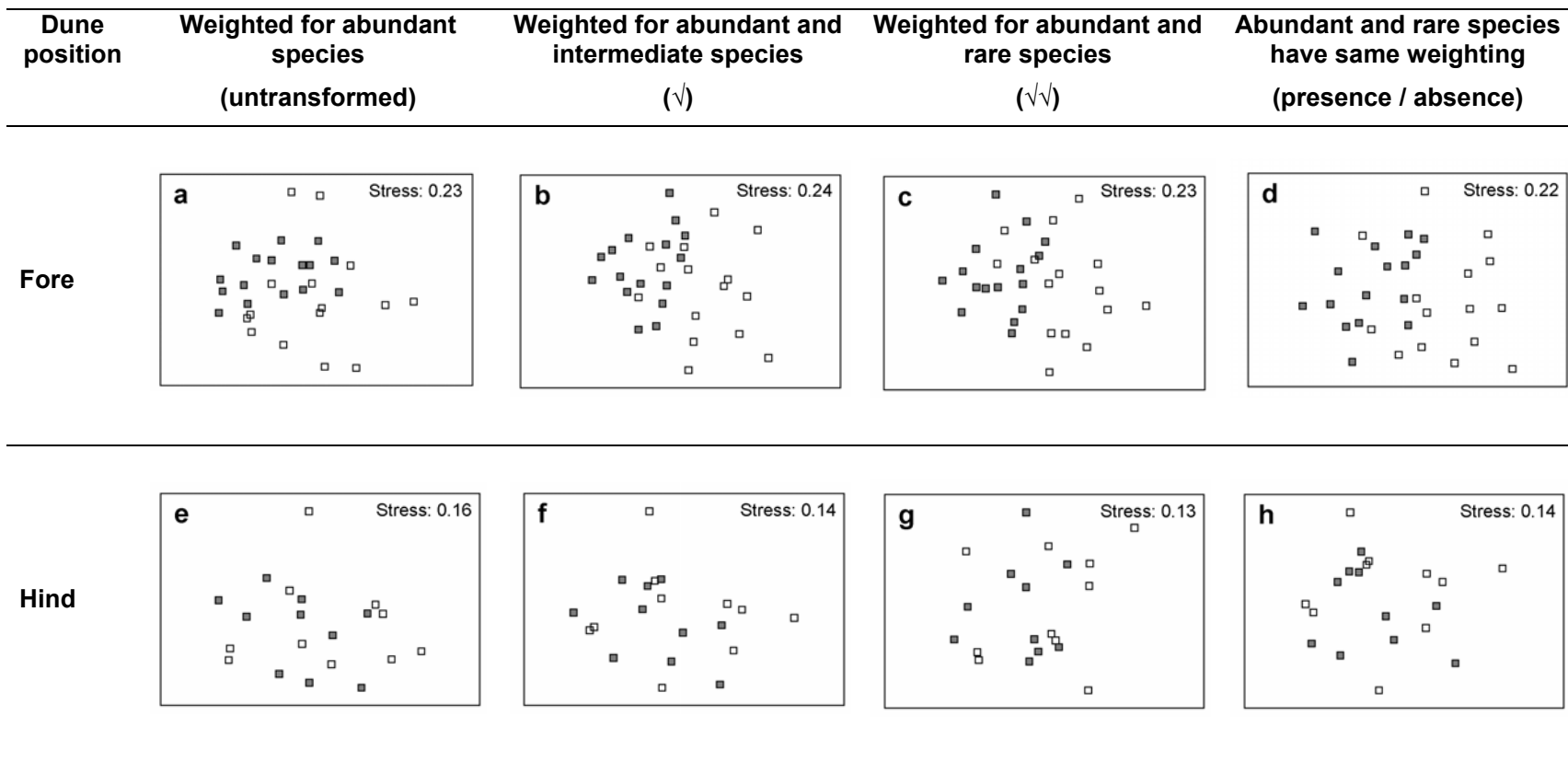


Figure 4.2: Two dimensional nMDS ordinations of fore and hind dune non-invaded (■) and bitou-invaded (□) sites illustrating different PERMDISP results (see Table 4.4): a-d and e-h show progressive down-weighting of abundant species using untransformed, square root and fourth root transformed and presence / absence data in fore and hind dune communities respectively.

Discussion

Changes to species richness within growth forms and vegetation structure following bitou invasion

Bitou invasion affected different complements of native growth forms in fore and hind dune communities. Functionally distinct native graminoid, native and exotic herb and native climber species were most affected by bitou invasion in fore dune communities. Bitou shading effects may competitively reduce richness of these low architecture herbaceous growth forms. As I hypothesised, bitou invasion shifted the distribution of vegetation structure in fore dune communities. Structural density was higher at the shrub level for bitou-invaded compared with non-invaded sites, reflecting increased bitou biomass following invasion. In contrast, structural density at the ground-cover level was lower for bitou-invaded compared with non-invaded sites. Invasion of bitou and replacement of small growth forms such as native graminoids and herbs may be responsible for the observed shifts in biomass distributions. Bitou invasion creates a dense shrub canopy which influences both light penetration to the soil surface and microclimate (Lindsay and French 2004). In turn, plant germination, growth and productivity are constrained by light quality and quantity. Following bitou invasion in fore dune communities, increased vegetation density at the shrub level reduces light penetration to ground level and may affect species regeneration (Olff et al. 1994; Rhazi et al. 2004). Low architecture herbaceous species with short generations may be expected to decline following bitou invasion as evidenced in fore dune communities.

Climber richness was also reduced in bitou-invaded compared with non-invaded fore dune communities. As climbers scramble over the shrub canopy, they will be less constrained by bitou shading effects than graminoids and herbs and adult survival may not be closely linked with bitou invasion. However, relatively short generation times of native climbers (e.g. *Stephania japonica* longevity is < 5 years (Clarke 1989)) and long

establishment of bitou in fore dunes (> 10 years) suggest that climbers may senesce at bitou-invaded sites without replacement.

In addition, novel disturbance regimes in the fore dune environment may limit recruitment opportunities for herbaceous species. Indeed a review by Turnbull et al. (2000) reported that herbaceous species were more seed limited than woody species. I recorded mining and fire disturbance at each site but did not record other disturbance regimes such as recreation activities, pollution and altered sand budgets which operate in the fore dune (Morley 1981; Viles and Spencer 1995; Brown and McLachlan 2002). Herbaceous species may therefore be affected by both invasion and disturbance and suffer reduced representation in fore dune environments. While native and exotic shrub species appeared unaffected by the invasion process in fore dune communities, shrub species richness was reduced in sites subject to sand mining. Woody species may therefore be intolerant of mining disturbance but may effectively compete with the functionally similar bitou bush in fore dune communities.

In contrast to fore dune patterns, hind dune bitou-invaded sites had reduced native shrub species richness when compared with non-invaded sites. Native shrub richness was also reduced at sites where sand mining had occurred. Native and exotic graminoid, herb and climber species richness values were unaffected by both invasion and mining processes. This finding indicates that outcomes in hind dune communities cannot be inferred from fore dune responses to bitou invasion. The presence of multiple overstorey layers (tree and shrub canopies) in hind dune communities may pre-adapt low architecture herbaceous species to bitou shading effects. Further, hind dune shrub compositions may be less competitive against bitou invasion than fore dune shrub compositions.

Similarly to fore dune vegetation, structural density was higher at the shrub level for hind dune bitou-invaded compared with non-invaded sites, reflecting increased bitou biomass following invasion. However, bitou invasion was also implicated in canopy-level changes to hind dune vegetation structure with canopy closure higher at non-invaded sites compared with bitou-invaded sites. This result may indicate that native canopy species are senescing in hind dune bitou-invaded communities and are not being replaced as bitou invasion suppresses or inhibits germination and seedling growth. Alternatively, canopy health may be reduced by bitou invasion. Long established bitou individuals use tree boles and branches as a physical support (T. Mason pers. obs.) and bitou biomass may cause breakages in the tree canopy. My observational dataset was unable to discount the possibility that hind dune sites were invaded *because* they had a sparser canopy rather than bitou invasion *causing* sparse canopy cover. Demographic studies and manipulation of bitou biomass may address this limitation.

My results indicated that a range of other exotic species were unable to exploit niches vacated by native species following bitou invasion. Similarly to native species, exotic herbs had reduced richness while exotic graminoid, climber and shrub species had unchanged richness in fore dune bitou-invaded compared with non-invaded sites. In hind dune communities, bitou invasion was not a significant predictor of richness within exotic growth forms. Similarly to my dune study, McIntyre and Martin (2002) found that many exotic and native species had similar responses to disturbance in sub-tropical eucalypt woodlands. In my case, bitou appears to be a superior competitor or stress tolerator compared with other exotic species.

Impacts of invasion on community variability are different in the fore and hind dune

Fore dune community variability results were consistent with my hypothesis that site-to-site variability increases if widespread or dominant species are most affected by

plant invasion. I found that a reduction in cover of common native species following invasion accounted for much of the dissimilarity between non-invaded and bitou-invaded sites. The lack of significance when using presence / absence data indicated that changed species cover rather than richness or identity drove variability responses. Dominant species are important in maintaining ecosystem functions such as productivity (Smith and Knapp 2003). While the compensatory role of the invader requires investigation, reduced abundance of dominant native species may reduce community resistance and stability (Smith and Knapp 2003). Increased variability of species cover abundances following invasion may disrupt dispersal and recruitment dynamics and ultimately feed back with further fluctuations in abundance patterns. I am unable to exclude the possibility that other factors such as latitude contributed to fore dune variability results. Low replication precluded consideration of latitudinal position as a factor in the analysis. However, if latitudinal effects were driving variability results, I would have expected consistent results across all transformations. Similar variability between bitou-invaded and non-invaded sites when species identity alone was considered indicated that variability results were most likely explained by invader effects.

In hind dune communities, variability was unchanged between non-invaded and bitou-invaded sites. Discrepancies in fore and hind dune results may relate to the presence of canopy cover in the hind dune which may limit invader effects (Hutchinson and Vankat 1997; Meiners et al. 2002; Setterfield et al. 2005). In addition, anecdotally, invasion is more recent in hind dunes than fore dunes, thus bitou impacts on hind dune species diversity may manifest as species senesce without replacement.

Conclusions

Invader effects such as loss of growth forms and increased site-to-site variability may affect ecosystem productivity. Graminoids, herbs and climbers in fore dune communities and shrubs in hind dune communities contribute to maximizing CO₂ uptake by filling gaps and creating three dimensional canopies which efficiently intercept light and increase productivity (Lawton 1994). In addition, root systems of herb, climber and shrub growth forms exploit different soil layers which collectively promote efficient uptake of water and nutrients (Troumbis and Memtsas 2000). Complementarity among species of diverse communities maximises resource utilisation (Tilman et al. 1996) and may inhibit invasion (Knops et al. 1999; Stachowicz et al. 1999). Indeed Fargione and Tilman (2005) found that diverse grassland plots better inhibited invasion than a monoculture of the most competitive species. Following invasion, replanting or reseeded efforts should focus on native graminoid, herb and climber species in fore dune communities and shrub species in hind dune communities to maintain ecosystem productivity and functioning.

I found that growth form analyses provided greater resolution than simple species richness in understanding the impacts of bitou invasion. A previous study found similar native species richness values between non-invaded and bitou-invaded hind dune sites (Chapter 3). However, the present study signalled that native shrub species richness was reduced at bitou-invaded sites. Richness within growth forms should therefore be measured in future monitoring programs.

In summary, the impacts of bitou invasion differed in fore and hind dune communities. The invader had different impacts on native plant growth forms, vegetation structure and community variability in fore and hind dune sites. While the concept of context-specific invasion outcomes has been reported elsewhere (Oriens

1986; Crawley 1987; D'Antonio 1993), the modulating effects of different resident communities on impacts of a single invader require further investigation (D'Antonio et al. 2000). Understanding invader impacts on native growth forms, vegetation structure and community variability informs restoration efforts following invader control.

Chapter 5

Moderate impacts of plant invasion and management regimes in coastal hind dune seed banks

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Introduction

Plant invaders are recognised as a major threat to the integrity of native communities across many biomes (Vitousek et al. 1997b, Mack et al. 2000) and control of these invaders has become an important conservation focus (Wittenberg and Cock 2005). Implicit in many invader management programs is the expectation that following control of the primary invader, regenerative capacity of soil seed banks will aid restoration. Indeed, soil seed banks, comprising all viable seeds on or in the soil or associated litter (Simpson et al. 1989), provide genetic storage that both reflect historic vegetation dynamics and contribute to future plant assemblages (Simpson et al. 1989, Warr et al. 1993). Consequently, investigation of soil seed banks may broaden our understanding of invasion impacts and assist in the prediction of restoration trajectories in managed communities.

The invasion process may affect soil seed bank dynamics indirectly by altering rates and composition of seed inputs from the standing vegetation (Hobbs and Mooney 1986), or directly by altering viability of soil-stored seed. High propagule pressure is recognised as an important attribute of many successful invaders (Williamson 1996). With the exception of invaders that spread vegetatively, I expect invader propagules to contribute to the seed rain, and if persistent, gain significant representation in the seed bank. In contrast, declines in native species richness have been demonstrated in a variety of communities following invasion (e.g. Drake et al. 1989, Levine et al. 2003)

and these declines may be expressed in the seed bank. Locally excluded native species may lose representation in the seed bank if they exhibit short-distance dispersal syndromes or short-term seed viability (Turnbull et al. 2000, Seabloom et al. 2003b). Further, native species which co-exist with the invader in the standing vegetation may suffer reduced reproductive output following competitive interaction with the invader (D'Antonio and Mahall 1991, Walck et al. 1999, Gould and Gorchoff 2000, Miller and Gorchoff 2004). In turn, these species may supply fewer seeds to the soil seed bank. In addition to changes in propagule supply, viability of existing seed bank components may be directly affected by the invasion process with changes to the physical and chemical environment. Dense invader canopies may dampen fluctuations in soil temperature and suppress germination (Baskin and Baskin 1998, Fenner and Thompson 2005 and references therein). Allelopathic compounds may also be leached or exuded from the invader, changing seed germination rates (Baskin and Baskin 1998, Grant et al. 2003). Overall, I expect that combined indirect and direct invader effects will reduce native seed bank richness and abundance.

Management regimes associated with control of the invader may also alter seed bank dynamics. Mechanical, chemical and biological control techniques reduce invader biomass (e.g. Erskine Ogden and Rejmánek 2005), fruit production or seed set and thus reduce the invader seed rain and abundance in the seed bank. Control activities which remove invader biomass may increase light penetration and stimulate germination, which in turn depletes the seed bank. Native seedling survival however, may be adversely affected by management due to off-target foliage damage by herbicide or trampling in follow-up control programs. Consequently, initial germination followed by low survivorship and seed production of germinants, may reduce native seed bank richness and abundance in managed communities. An alternative view is that

management may release native species from root or shoot competition with the invader in turn enhancing seed production and seed bank inputs. I therefore predict that invader management programs will impact seed bank dynamics; however the direction of impact is unclear.

I investigated plant invasion and management impacts on soil seed banks using bitou bush (*Chrysanthemoides monilifera* ssp. *rotundata* (DC) Norl.), hereafter termed bitou, a South African shrub which has invaded coastal dune communities of eastern Australia. Bitou adversely affects dune communities by out competing dominant native species (Weiss and Noble 1984a, b), threatening biodiversity values (*New South Wales Threatened Species Conservation Act 1995*) and altering nutrient cycling by changing litter quality (Lindsay and French 2004) and quantity (Lindsay and French 2005). Bitou management typically involves mechanical, chemical or biological control (Weiss et al. 1998) with follow up control of bitou germinants and secondary weed invasions (Weiss et al. 1998). While replanting and reseedling of native species are undertaken at some localities, managers often rely on germination of native individuals from the seed bank to replace bitou individuals. However, seed bank dynamics of heavily-invaded dune communities and restoration potential of sites subject to bitou management are yet to be quantified.

In this study, I investigated the richness, abundance and composition of soil seed banks at heavily-invaded, managed and sparsely-invaded hind dune forest sites. I also assessed similarity of the standing vegetation and seed bank. These comparisons aimed to highlight legacies of invasion in the seed bank and predict restoration potential of managed sites.

Methods

Study area

I conducted the study on the north coast of New South Wales in hind dune open to closed woodland / forest vegetation (28° 25' 45" S; 153° 33' 25" E to 32° 46' 27" S; 152° 2' 48" E) (Figure 5.1). The standing vegetation commonly comprised overstorey dominants such as *Banksia integrifolia*, *Angophora costata* and *Corymbia intermedia*, midstratum species such as *Banksia serrata* and *Monotoca elliptica* and lower stratum species such as *Pteridium esculentum*, *Lomandra longifolia* and *Oplismenus aemulus*. In order to estimate the minimum age of invasion, I made counts of bitou growth rings from the oldest individuals at each invaded site. This measure is conservative as only extant individuals were recorded. The maximum number of growth rings at each site ranged from 12 to 29. Assuming annual growth cycles, I concluded that bitou established at least 10 years ago at heavily-invaded sites. Land manager records indicated that bitou invasion occurred >20 years ago at managed sites. Managed sites had variable control histories ranging from recent activities (<5 years) to long term control works at a site (16-20 years).

Field methods

I collected soils samples from 15 study sites each comprising a 20 x 50 m (0.1 ha) quadrat in February and March 2004 after many species had finished fruiting and seed-release. Standing vegetation had previously been surveyed (Chapter 3). Sites were categorised as: (1) sparsely-invaded ($n = 5$) which had little bitou cover (average 5 %) and no history of control activities, (2) managed ($n = 5$) which had active control of bitou invasion predominantly through labour-intensive control techniques such as backpack and vehicle spraying, direct herbicide application to stems and hand removal, and (3) heavily-invaded ($n = 5$) which had significant bitou cover (average 60 %) and no history of control activities. I was unable to locate hind dune sites completely devoid

of bitou in the standing vegetation. I used sparsely-invaded sites, where bitou was represented by isolated mature individuals within or adjacent to sites, as a best estimate of native reference conditions. This site selection, while not ideal, does indicate that sparsely-invaded sites are capable of invasion and are not inherently different from managed and heavily-invaded sites.

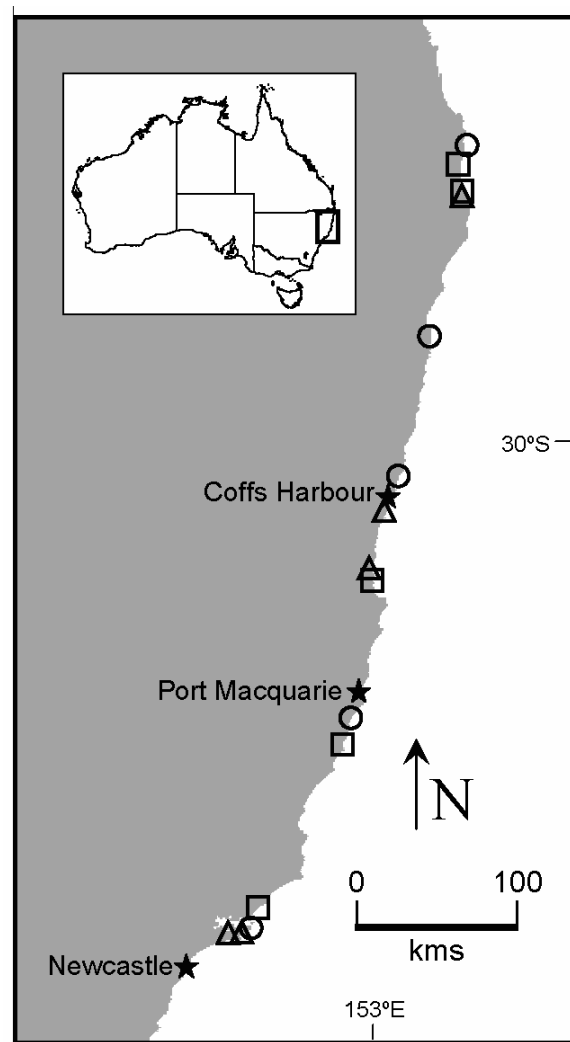


Figure 5.1: Map of hind dune site locations along the New South Wales coastline:
 Sparsely-invaded = \square ; Managed = \circ ; Heavily-invaded = \triangle ; Major city = \star

Soil corer dimensions and number of core samples were optimised for surveying hind dune seed banks in a pilot study conducted in November 2003 at a mid north coast heavily-invaded hind dune site (32° 46' 32" S; 152° 2' 4" E) which I expected would yield a conservative soil-stored seed bank. I extracted 149 cores from the site (corer diameter = 63 mm), separated into two depths: 0-50 mm and 51-100 mm. Species richness was significantly higher at the top of the soil profile (0-50 mm) compared with soil extracted at 51-100 mm ($F_{1, 144} = 22.032$; $P < 0.001$), and 79% of species (71% of seeds) from 0-100 mm depth were in the top 50 mm. Such a result conforms with other Australian studies in sclerophyllous vegetation where seed was concentrated at the top of the soil profile (Auld 1986, Koch et al. 1996, Grant and Koch 1997). Consequently, I chose to sample to 50 mm in the main experiment. I constructed a species area curve to determine an optimal number of cores to be extracted at a site (Greig-Smith 1983). I chose to collect 100 cores which captured an average of 22 species (± 0.852 SD) from a total of 27 species in the pilot study. At each site, cores were then randomly extracted and litter was excluded to maintain constant sampling volumes across sites. Bulked cores for each site were stored away from direct sunlight and transferred to glasshouses within three weeks of field collection. The total soil volume for each site was 0.016 m^3 .

Seedling emergence was used to estimate the viable soil seed bank (Simpson et al. 1989). While I acknowledge that reliance on seedling emergence may not record seed exhibiting induced or enforced dormancy (Hutchings 1986), this method was employed due to its efficiency in community-level studies (Simpson et al. 1989).

Potential germination cues for sclerophyllous plant species have been investigated in numerous Australian studies (e.g. Purdie 1977, Auld and O'Connell 1991, Roche et al. 1997). I trialled three potential cues of heat, smoked water, and combined heat and smoked water along with a control (regular watering alone) in a

second pilot study. The smoked water treatment and the control yielded similar germination results. However, heat treatments significantly reduced germination ($F_{1,28} = 453.156$; $P < 0.001$). The combination of heat and smoked water yielded similar germination results to those of heat alone. I chose to apply smoked water alone as a germination cue in the main study for two reasons: (1) smoked water was not detrimental to germination in the pilot study, and (2) positive effects of smoke on germination have been reported in other studies (de Lange and Boucher 1990, Roche et al. 1997). The smoked water was produced following the method of Dixon et al. (1995). A mixture of leaf litter, bark, fine stem material and fresh foliage (total weight: 318 g) from a hind dune *Eucalyptus botryoides* / *Banksia integrifolia* woodland community was used as fuel. The smoke generated during combustion was bubbled through a 20 L container of distilled water for 90 minutes. The smoked water concentrate was then diluted for treatment application using 1 part concentrate to 10 parts water (Read and Bellairs 1999). One batch of smoked water was used, and, while this approach is not ideal (Morrison and Morris 2000), time constraints prohibited production of batches for each replicate.

Bulked cores for each site were mixed, sieved (using a 6 x 6 mm mesh) and distributed evenly among 18 seedling propagation trays (340 mm x 290 mm). Each tray had a 1:1 vermiculite / perlite base which was covered with the sample soil to a depth of approximately 10 mm. Trays were placed in a randomised block design (three trays per site per block) in glasshouses over two days in early March 2004. Thereafter, trays were periodically re-randomised in each block. Trays were watered with smoked water for the first four days of the experiment to allow sufficient contact of smoke particles with seed in the soil. Trays were then watered twice daily. Seedling emergence was monitored weekly for the first six weeks, then fortnightly for the next three months,

then monthly until the experiment terminated a year later in March 2005. Duplicate seedlings were removed from trays after counting. Each species was removed after flowering or once positively identified. Glasshouse temperatures were monitored using iButton® temperature dataloggers (Maxim Dallas Semiconductor). Recorded temperatures ranged from 5° C (July 2004) to 40.5° C (December 2004). A control tray composed of river sand (with perlite/vermiculite base) was placed in each block to detect glasshouse contaminants which were removed from analyses.

Data analysis

I conducted two-factor ANOVAs (without interaction) to analyse the effects of invasion category (fixed effect) and glasshouse block (random effect) on the dependent variables of native and weed species richness and abundance, bitou abundance and native growth form species richness (graminoid, herb, shrub, tree and climber classes). Weeds were defined as species introduced to the New South Wales coastal zone. Block was consistently non-significant in the ANOVA indicating that location in the glasshouse did not affect seed bank germination. Consequently, I recalculated species richness values and used a one-factor ANOVA to test the effect of invasion category on the dependent variables. Growth form information was obtained from *The Plant Information Network System of the Botanic Gardens Trust v2.0* (<http://plantnet.rbgsyd.nsw.gov.au/>) and analyses were conducted using SPSS (2003). I tested homogeneity and normality of error variances using visual inspection of residual plots (Grafen and Hails 2002) and the Shapiro-Wilk test (Miller 1997) respectively, and data were square root or log transformed where necessary. I used Tukey's test for post hoc pairwise comparisons.

I tested the hypothesis that species compositions were similar across different invasion categories for north coast hind dune communities using a one-way analysis of

similarity (ANOSIM) on square root transformed abundance data. This procedure generated a Bray-Curtis similarity matrix within the PRIMER package (Clarke and Warwick 2001). To examine whether invasion categories differed solely because of invasion by bitou, or whether other compositional changes were evident, the data were analysed after bitou abundance values had been omitted.

I used Sørensen's quotient of similarity (QS) (Sørensen 1948) to investigate similarities between standing vegetation and soil-stored seed banks, having surveyed the standing vegetation as part of an earlier study (Chapter 3). The quotient was calculated as follows:

$$QS = \left(\frac{2C}{A + B} \right) * 100$$

where C is the number of species common to the standing vegetation and seed bank, and A and B are the number of species in the standing vegetation and seed bank respectively.

Results

I recorded 156 plant species from 51 families in the seed bank of 15 hind dune sites (Appendix C). Thirty-eight of the 156 recorded species were weeds.

Bitou abundance varied significantly with invasion category (Table 5.1). Pairwise comparisons revealed that heavily-invaded sites had the highest bitou abundance with an average of 37 germinants / m² to a depth of 50 mm. Sparsely-invaded and managed sites had significantly lower bitou abundance (Figure 5.2). In contrast, overall native and weed species abundances were similar across all invasion categories.

Table 5.1: One-factor ANOVAs comparing the effect of invasion category on native and weed species richness and abundance, bitou abundance and native graminoid, herb, shrub, tree and climber richness in hind dune soil seed banks.

Dependent variable	F_(2,12)	P value
Native species richness	1.590	0.244
Weed species richness	3.634	0.058
Native species abundance	1.059	0.377
Weed species abundance	3.109	0.082
Bitou abundance	8.521	0.005
Native graminoid richness	0.975	0.405
Native herb richness	0.229	0.799
Native shrub richness	1.348	0.297
Native tree richness	10.647	0.002
Native climber richness	0.250	0.783

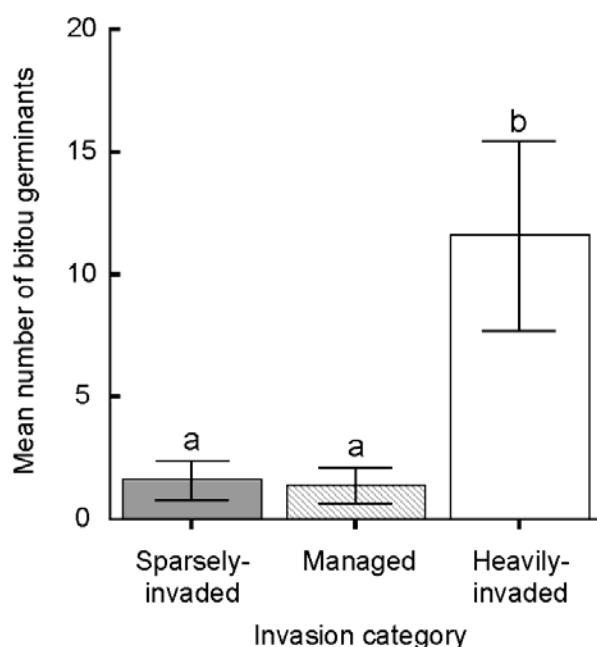


Figure 5.2: Mean number of bitou germinants for each invasion category in hind dune seed banks (\pm one standard error). Different letters indicate significantly different values according to the post hoc pairwise Tukey's test.

Native tree species richness also varied significantly with invasion category (Table 5.1). Pairwise comparisons indicated that sparsely-invaded sites had the highest native tree species richness with managed and heavily-invaded sites supporting significantly fewer tree species in the seed bank (Figure 5.3). Native graminoid, herb, shrub and climber species richness along with overall native species richness were

similar across invasion categories. Weed species richness did not vary significantly with invasion category (Table 5.1), however, a trend of managed and heavily-invaded sites supporting higher weed species richness (mean \pm standard error: 10.00 ± 0.55 and 10.00 ± 0.71 respectively) than sparsely-invaded sites (7.40 ± 1.03) was evident. A number of significant environmental weeds were represented in the seed bank and included *Lantana camara* and *Baccharis halimifolia* (Table 5.2). However, the majority of germinable weed seeds belonged to incidentals such as *Conyza* spp. and *Gamochaeta* spp. These species are non-native but are not currently considered invasive in natural systems.

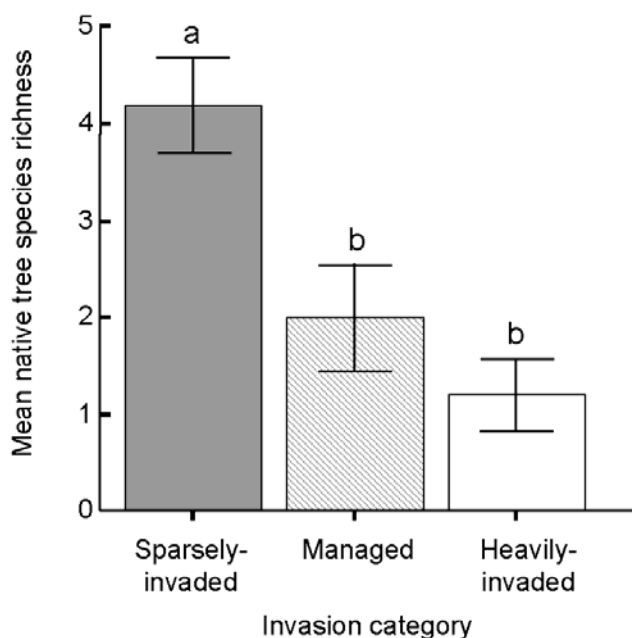


Figure 5.3: Mean tree species richness for each invasion category in hind dune seed banks (\pm one standard error). Different letters indicate significantly different values according to the post hoc pairwise Tukey's test.

Table 5.2: Abundance of weed species for each invasion category in hind dune seed banks.

Weed species	GF	Species abundance		
		M	H-I	S-I
<i>Conyza bonariensis</i> (L.) Cronquist	h	1810	8	10
<i>Gamochaeta pensylvanica</i> (Willd.) Cabrera	h	718	193	34
<i>Gamochaeta calviceps</i> (Fernald) Cabrera	h	260	6	0
<i>Solanum nigrum</i> L.	h	98	2	2
<i>Conyza parva</i> Cronquist	h	37	8	0
<i>Gamochaeta americana</i> (Mill.) Wedd.	h	25	51	1
<i>Conyza sumatrensis</i> (Retz.) E. Walker	h	23	55	32
<i>Polygala myrtifolia</i> L.	s	12	0	0
<i>Bidens pilosa</i> L.	h	10	1	0
<i>Crassocephalum crepidioides</i> (Benth.) S. Moore	h	9	6	10
<i>Andropogon virginicus</i> L.	g	8	12	3
<i>Chrysanthemoides monilifera</i> ssp. <i>rotundata</i> (L.) Norl.	s	7	58	8
<i>Aster subulatus</i> Michx.	h	7	0	4
<i>Lantana camara</i> L.	s	4	2	0
<i>Ehrharta erecta</i> Lam.	g	4	0	1
<i>Rivina humilis</i> L.	s	4	0	0
<i>Baccharis halimifolia</i> L.	s	3	4	2
<i>Facelis retusa</i> (Lam.) Sch. Bip.	h	3	0	0
<i>Polypogon littoralis</i> J.C. Sm.	g	2	3	3
<i>Senecio madagascariensis</i> Poir.	h	2	3	0
<i>Hypochaeris radicata</i> L.	h	1	4	0
<i>Polycarpon tetraphyllum</i> (L.) L.	h	1	4	1
<i>Richardia humistrata</i> Cham. & Schltdl.) Steud.	h	1	1	0
<i>Centaurium erythraea</i> Rafn	h	1	0	0
<i>Solanum seaforthianum</i> Andrews	c	1	0	0
<i>Stenotaphrum secundatum</i> (Walter) Kuntze	g	1	0	0
<i>Sonchus oleraceus</i> L.	h	0	7	4
<i>Aira cupaniana</i> Guss.	g	0	3	0
<i>Ageratina adenophora</i> (Spreng.) R.M. King & H. Rob.	h	0	3	1
<i>Erechtites valerianifolia</i> (Wolf) DC.	h	0	1	0
<i>Verbena bonariensis</i> L.	h	0	1	7
<i>Amaranthus blitum</i> L.	h	0	0	1
<i>Axonopus fissifolius</i> (Raddi) Kuhlman	g	0	0	1
<i>Cerastium glomeratum</i> Thuill.	h	0	0	1
<i>Cyperus brevifolius</i> (Rottb.) Hassk.	g	0	0	29
<i>Galinsoga parviflora</i> Cav.	h	0	0	1
<i>Solanum mauritianum</i> Scop.	t	0	0	4
<i>Taraxacum officinale</i> Weber	h	0	0	1
Total number of weed seeds		3052	436	161
Total weed species richness		26	23	23

GF = growth form: g = graminoid, h = herb, s = shrub, t = tree, c = climber; M = Managed, H-I = Heavily-invaded, S-I = Sparsely-invaded.

I found that seed bank species compositions were similar across all invasion categories (Global $R = -0.009$; $P = 0.485$). However, when seed bank and standing vegetation compositions were compared, similarity was low for all invasion categories (Table 5.3). This suggests that seed banks are poor predictors of mature vegetation composition in hind dune communities. A number of serotinous species (Lamont et al. 1991) were dominant in the standing vegetation. These species store seed in structures above ground and therefore have low representation in the seed bank. However, removal of serotinous species from the analysis did not greatly affect similarity values (data not shown).

Table 5.3: Sørensen's quotient of similarity comparing standing vegetation and seed banks for each invasion category (n = 5) (\pm one standard error).

Invasion category	Mean similarity \pm se
Sparsely-invaded	30.63 \pm 5.10
Managed	28.09 \pm 2.20
Heavily-invaded	28.69 \pm 2.05

Discussion

I found that plant invasion and management regimes had apparently moderate impacts on hind dune seed banks.

Effects of invasion and management on bitou seed banks

As predicted, heavily-invaded sites supported significantly higher bitou abundance than sparsely-invaded sites, probably reflecting a change in invader propagule pressure and seed bank dynamics. Importantly, managed sites were similar to sparsely-invaded sites with low bitou abundance. This implies that management effectively targeted bitou propagule pressure and reduced the probability of future re-invasion. My findings agree with a study of mechanical and fire-related removal of *Acacia* invaders in South African fynbos (Holmes et al. 1987) where management

reduced, but did not eliminate *Acacia* seed banks. However, my findings contrast with a North American grassland restoration project where the seed bank of *Agropyron cristatum*, an introduced grass, was unaffected by herbicide or clipping control techniques (Ambrose and Wilson 2003, Wilson and Pärtel 2003). The disparate results may be explained by higher seed production and seed banks of *A. cristatum* relative to bitou. In addition, incomplete control of *A. cristatum* was postulated as reducing intraspecific competition, thereby increasing per capita seed production (Ambrose and Wilson 2003).

My finding that bitou was represented in the sparsely-invaded seed bank may reflect propagule pressure both of extant, isolated bitou individuals and of seed dispersed by vertebrates (Gosper 2004) from bitou invasion in the surrounding landscape. The presence of bitou seed in sparsely-invaded seed banks indicates that bitou seed availability alone does not determine the degree of invasion of hind dune communities. Rather, above-ground dynamics governing germination or seedling competition may suppress bitou invasion at sparsely-invaded sites. Sparsely-invaded sites may also have few disturbance events to provide resource pulses and invasion opportunities (Johnston 1986, Davis et al. 2000). Management must therefore seek not only to reduce bitou seed availability, but also to minimise disturbance which may provide competitive advantage or germination opportunities for bitou propagules.

Although seed availability alone may not drive the degree of hind dune invasion, it may be important in determining invasion densities. My finding of an average of 37 bitou germinants / m² at heavily-invaded sites contrasts with a study by Weiss (1984) who reported densities of viable bitou seed two orders of magnitude greater (2 000 – 3 000 seeds / m²) than the present study. Weiss (1984) measured seed density to a greater depth than the present study (100 mm rather than 50 mm), sampled from directly

below bitou individuals rather than randomly throughout the site and directly tested viability of seed recovered from soil samples rather than using seedling emergence techniques. I investigated the discrepancy in bitou seed bank densities between my study and Weiss (1984) by collecting a further 100 cores from one heavily-invaded site and directly counting bitou seed in the soil. I found 103 intact seeds / m², indicating that my experiment had a germination rate of 36%. This result agrees with a study by Aveyard (1971) which found low germination rates (< 50 %) of bitou seed under a range of environmental conditions and reported erratic germination under nursery conditions. Consequently, while many more dormant or non-viable bitou seeds may be present in soil-stored seed banks, my analysis only recorded the readily germinable fraction.

It is also possible that the dramatic reduction in bitou seed banks I reported here compared with Weiss's (1984) study 20 years earlier may reflect increased biocontrol activity through the study area. The first biocontrol agents for bitou were released in 1987 (Stuart et al. 2002) after Weiss's (1984) study. Biocontrol agents have dispersed along most of the New South Wales coastline (Edwards et al. 1999, Holtkamp 2002) with variable success in reducing bitou seed production or viability (refer to Holtkamp 2002, Stuart et al. 2002). During my direct count of the bitou seed bank, I found three seeds which appeared affected by the seed fly and many fragments of bitou seed. Clearly, evaluation of total biocontrol effects on bitou seed banks is required.

Effects of invasion and management on secondary weed seed banks

I found a trend of higher weed richness at heavily-invaded and managed sites compared with sparsely-invaded sites. This trend may indicate that secondary weed propagules accompany bitou invasion rather than invading with subsequent management activities: disturbance regimes which facilitate primary bitou invasion may

also facilitate secondary weed representation in the seed bank. Much of the weed component of the seed bank was characterised by ruderal, herbaceous species. Such species pose few conservation concerns because they are rapidly replaced following disturbance as processes of canopy closure, litter accumulation and plant competition occur (Appleby 1998). However, a number of significant secondary weed species such as *Lantana camara* were also represented in the seed bank. *L. camara* has been nominated among the 100 worst invaders globally (<http://www.issg.org/database>) and may threaten conservation of hind dune communities. The invasion potential of secondary invaders in the seed bank indicates a need to conduct follow-up control in managed sites.

Effects of invasion and management on native seed banks

Richness of native tree species in seed banks at heavily-invaded sites was significantly lower than richness values in seed banks at sparsely-invaded sites, signalling a shift in community structure. In a separate study of above-ground vegetation, sparsely-invaded sites had a denser canopy than heavily-invaded sites (Chapter 4). Consistent with my predictions, this may signal poor canopy health and reproductive output in the standing vegetation of heavily-invaded sites, which may in turn be expressed in reduced representation of tree species in the seed bank. Seed banks of managed sites had similar tree richness values to heavily-invaded sites which may be a legacy of invasion or a consequence of management practices. Reduced richness of tree species in the seed bank may result in future canopy gaps in managed hind dune communities. Canopy cover has been recognised as important in community resilience to invasion (Meiners et al. 2002, Setterfield et al. 2005) and reduced tree richness in seed banks at managed sites may indicate susceptibility to future re-invasion events.

While the study detected differences among sites with regard to native tree richness in seed banks, overall native species richness, abundance and composition along with graminoid, herb, shrub and climber richness, were similar across seed banks at all sites. This result was inconsistent with my prediction that native seed bank richness and abundance decreases with increasing invasion intensity and either decreases or increases following management. It appeared that, with the exception of tree species, the native seed bank was largely unaffected by invasion and management. Conversely, if soil seed banks are long-lived, insufficient time may have elapsed since invasion and subsequent management to observe native seed bank depletion (refer to Warr et al. 1994).

However, low similarity between standing vegetation and seed banks indicated that the full complement of hind dune propagules was not captured in the seed bank. My findings correspond with an invasion study by Holmes and Cowling (1997b) which found that fynbos sites long-invaded by *Acacia saligna* and non invaded fynbos sites had low similarity between seed banks and standing vegetation (Sørensen's quotient: 10-30.6% and 20.9-31.4% respectively). These low similarity values contrast with other vegetation communities. Henderson et al. (1988) reported a quotient of 88.9% for desert grasslands while Bekker et al. (1999) found similarities of 60-70% for dune slack grasslands. While these communities have greater similarity between the standing vegetation and seed bank compared with my study, it is difficult to directly compare the similarity quotients due to differences in sampling methodology. This is a common problem in seed bank studies (Simpson et al. 1989).

A number of species dominant in the standing vegetation were absent from the seed bank. Species of the Proteaceae and Myrtaceae families exhibit serotiny (Lamont et al. 1991) where seed banks are stored above-ground on the plant. However, serotiny

alone did not explain the divergence in composition of the seed bank and standing vegetation. Other species absent from the seed bank may have short-term seed viability and form part of the transient seed bank (Thompson and Grime 1979). These species may have effective dispersal mechanisms and rely on the annual seed rain for propagules to opportunistically germinate. In addition, plants such as graminoid and herb species (e.g. *Dianella caerulea*) may invest in vegetative spread over sexual reproduction and therefore contribute few propagules to the hind dune seed bank (see Hayashi and Numata 1975 for a related discussion). My study may have also missed species which are difficult to germinate. While soil seed banks offer storage for species with persistent seeds, those species that rely on vegetative propagation, or have transient seed banks or alternate storage modes, may not maintain representation.

I have inferred invader and management effects using a comparative mensurative approach (Hurlbert 1984) which cannot provide conclusive proof of impacts. This comparative rather than experimental (e.g. BACI design) approach was necessary as I wished to infer impacts over a time-scale relevant to management: I measured seed bank status a number of years after invasion or first application of management thus improving my ability to detect changes in processes such as reproductive output and pollinator dynamics over a number of seasons. Long-term, large-scale experimental manipulations would confirm my inferences, however sustained commitment to such experiments is difficult to achieve (Bennett and Adams 2004).

Management implications

A number of implications for conservation management emerge from this study. Low similarity between seed bank and standing vegetation compositions suggests that managers cannot rely exclusively on soil-stored seed banks to restore pre-invasion

conditions. Responses to invasion and management by native propagules with transient seed banks or alternate storage modes require investigation to provide full understanding of dune regeneration potential. However, with the exception of tree species, natives with persistent seed banks appeared largely unaffected by both bitou invasion and management in hind dunes. Native tree propagules may require supplementation via planting or seeding operations in heavily-invaded and managed communities, but, with appropriate germination cues, remaining species with persistent seed banks may naturally regenerate following invasion and management.

This seed bank study has also highlighted considerable regeneration potential of secondary invaders. Disturbance which facilitated primary invasion or disturbance associated with control activities may also allow secondary invader representation in the seed bank. Consequently, secondary invasion may accompany native regeneration. Continued removal of secondary invaders prior to flowering should exhaust their seed bank reserves.

Chapter 6

Do graminoid and woody invaders affect community assembly equally?

Introduction

Assembly rules have been proposed to explain or predict which species combine to form a community (Diamond 1975, Keddy 1992). These rules relate to (1) internal dynamics such as interspecific competition and co-existence, (2) environmental constraints such as supply of space, energy and nutrients and (3) dispersal constraints such as viability of stored propagules (Belyea and Lancaster 1999). Invasive species have significant effects on internal dynamics through competitive and non-competitive interactions with residents (Levine et al. 2003, Seabloom et al. 2003b), and may transform environmental parameters such as nutrient levels, fire regimes and decomposition rates (Vitousek 1990, D'Antonio and Vitousek 1992, Lindsay and French 2004, 2005). Invaders may also disrupt pollination or seed dispersal dynamics of resident species (Hobbs and Mooney 1986, Chittka and Schürkens 2001). These findings suggest that invaders are important determinants of community assembly and may operate as biotic filters by selecting against some species in the community more than others. Where plant invaders establish in response to a disturbance which modifies or destroys the original vegetation, the invader may influence community re-assembly or recolonisation. Where invasion occurs in the absence of disturbance, the invader may influence community disassembly or species loss. In both cases, the invader may select against representation of particular plant traits. In this study, I asked whether invaders consistently select against particular plant traits in a range of community types, and therefore cause predictable, directional changes to invaded communities.

Numerous individual studies have documented invader impacts on native communities, generally using species richness as a measure of impact (Tilman and Lehman 2002, Wilsey et al. 2005). However, the relative sensitivity of particular traits to major invaders under natural conditions is poorly understood (Ortega and Pearson 2005). Existing invasion datasets provide an opportunity to examine trait response to invasion rather than focussing solely on species richness. This more detailed approach should reveal particular plant traits that are consistently filtered out of a community by an invader, and therefore improve our ability to predict the effects of invasion across communities for a range of different invaders. This approach would also allow prediction of trajectories of species loss and inform targeted reseedling or replanting programs following control of the invader.

Graminoid or woody species have often become dominant invaders of natural systems and I predicted that the different morphologies of these invaders would result in different invasion effects on resident communities. For instance, graminoid invaders may directly affect resource availability in resident communities through rapid growth, which reduces light penetration at the soil surface affecting growth of other herbaceous species (Thompson and Harper 1988). Graminoid invaders may also indirectly affect the resident community by changing litter quality (Evans et al. 2001) and by altering fire regimes (D'Antonio and Vitousek 1992, Rossiter et al. 2003). Graminoid invaders have a low, tufted or spreading growth form and dense, shallow root systems that sequester resources high in the soil profile (Harper 1977, D'Antonio and Vitousek 1992). In contrast, woody invaders attain greater heights and deeper rooting profiles than graminoid invaders. They increase biomass, shift growth form dominance and reduce structural diversity of invaded communities (Braithwaite et al. 1989, Richardson 1998). Woody invaders may also shade out short, herbaceous species (e.g. Hobbs and Mooney

1986, Wearne and Morgan 2004) and suppress recruitment of native woody species (Merriam and Feil 2002).

I used meta-analysis as a quantitative, objective and replicable method to summarise multiple invader impact studies, in search of general filtering effects by invaders. While qualitative reviews of the invasion literature indicate substantial invader effects (e.g. Gordon 1998, Mack and D'Antonio 1998), vote-counting and narrative reviews do not consider sample size and statistical power and may therefore reach erroneous conclusions (Gurevitch and Hedges 1993). Meta-analysis combines studies by calculating effect sizes that are independent of both sample size and the scale of measurement used in each study (Gurevitch and Hedges 1993).

The meta-analysis assessed the filtering effect of graminoid and woody invaders on resident communities by analysing the effects of invasion on species richness in various vegetative and reproductive plant traits categories. I used meta-analysis to examine the strength and consistency of response across communities in a variety of biomes. I examined graminoid and woody invader classes, and tested for evidence of their effects on two vegetative traits (growth form and longevity) and two reproductive traits (seed mass and flowering phenology). I tested the following hypotheses:

H1A: *That invaders will have the strongest effect on growth forms similar to themselves;*

H1B: *That woody invaders will affect a wider range of growth forms than graminoid invaders;*

Background: According to theories of niche differentiation and species co-existence, individuals with similar traits will compete most strongly (Fargione and Tilman 2005 and references therein) and inferior competitors will be excluded. Ultimately species may co-exist through differentiation of attributes in niche space (Harper 1977). I

therefore expected that if invaders dominate via competitive mechanisms, they will most severely affect similar growth forms: native graminoids will be most affected by graminoid invaders and native shrubs and trees will be most affected by woody invaders. I also expected woody invaders to consistently and negatively affect a greater range of native growth forms than graminoid invaders. The greater shoot height of woody compared with graminoid invaders allows woody species to grow above the graminoid and herb layer and pre-empt light resources (Heisler et al. 2004, Cole and Weltzin 2005).

H2A: *That species across longevity classes will be affected by invasion – the degree and direction of impact for each class are unclear;*

H2B: *That woody and graminoid invaders will have similar effects on native longevity classes;*

Background: At the start of each growing season, perennials have well-established root systems along with energy and nutrient stores (Tilman 1988). Consequently, perennials may be less affected by woody or graminoid invaders than short-lived annual and biennial species which must establish from seedlings. Similarly, some long-lived perennials may represent founder populations which pre-date the invasion event and therefore appear less affected by invasion than annual or biennial species. According to these observations, I would expect both woody and graminoid invaders (which are mostly perennials in the meta-analysis) to affect short-lived plants (obligate annuals and biennials) more severely than perennials.

Conversely, short-lived plants may be advantaged under highly disturbed conditions where storage, as dormant seed, buffers against environmental stochasticity (Harper 1977). Invasion often accompanies disturbance (Hobbs and Huenneke 1992)

and under such circumstances, I may expect short-lived plants to be less affected than perennials by woody or graminoid invaders.

H3A: *That woody and graminoid invaders will favour representation of large- relative to small-seeded species in invaded communities;*

H3B: *That woody invaders will have a greater impact on both large- and small-seeded species relative to graminoid invaders;*

Background: Large-seeded species generally tolerate stress such as shade better than small-seeded species (Westoby et al. 1992 and references therein). Large seed size may also aid seedling development through a thick litter layer because larger seeds have more reserves to grow through the litter to the light, and to develop roots to penetrate into the soil. Further, seedlings from large seeds may increase in height more quickly and out-compete small-seeded seedlings (Tilman 1988).

I also predicted that the greater canopy height, and therefore shading effects, of woody invaders would increase their effect on both large- and small-seeded species relative to graminoid invaders.

H4: *That sympatric native species whose flowering phenology is synchronous with the invader will be more affected (either negatively or positively) by the invader than species whose flowering phenology is asynchronous with the invader;*

Background: Plant invaders may reduce pollination success in native communities by competing for pollinator services thereby reducing frequency of visits, pollen quantity and ultimately seed set in native species (Chittka and Schürkens 2001, Ghazoul 2002). Alternatively, invaders may facilitate pollination in native species: flowering of the invader may attract pollinators which also service other species in the area (Rathcke and Lacey 1985). Plant invaders may also reduce pollination success of native species by deposition of heterospecific pollen on stigmas of native individuals (Brown and

Mitchell 2001) which can interfere with pollination and fertilisation in a number of ways: pollen allelopathy, clogging or closing of the stigma, stylar inhibition (see Brown and Mitchell 2001 and references therein) and pre-emption of ovules.

I addressed potential pollinator competition or facilitation by the invader through analysing invasion and response by biotically pollinated species only. In contrast, I used both biotically and abiotically pollinated species to observe species response to interspecific pollen transfer by invasive species.

Methods

The data included in the meta-analysis consisted of observational studies which measured the impact of a graminoid (perennial/annual) or woody (shrub/tree) invader on species richness within plant traits. I located studies by using database searches and examining paper reference lists. I used the following criteria to select studies: (1) each study needed to focus on a single invader or growth form and its impacts at the community level. While communities were predominantly native, incidental exotics at low abundance were sometimes recorded – these exotics were removed from analyses; (2) studies were observational rather than manipulative and examined both invaded and non-invaded sites; (3) as most studies reported species richness results rather than diversity within plant traits, original databases were generally required to categorise species into plant traits. I therefore relied on author compliance in providing original datasets.

The meta-analysis used data from 20 studies conducted at 31 different locations (Table 6.1). In some cases I reported multiple results from single studies which may violate assumptions of independence, however, the loss of information may be a more serious problem than non independence (Gurevitch et al. 1992). In order to address power and interdependence issues, I conducted primary meta-analyses (which included

multiple results) and I then evaluated the effect of interdependence by performing additional, less powerful site-level meta-analyses (where only one site per study was included) to determine whether the patterns seen in the primary meta-analyses were affected by non independence. Four different iterations of each meta-analysis were performed using a different single result each time for studies with multiple results. Where site-level results consistently differed from results of primary meta-analyses, I present both findings.

Species from each dataset were categorised into plant traits using published botanicas and electronic databases (Appendix D). The study was restricted to using only well-documented plant traits for classifications (Table 6.2) because measurement of traits such as specific leaf area, litter quality etc. for each species was unfeasible. All plants were categorised according to their adult classification although individuals may not have reached adult potential in each database. In order to increase power of the meta-analysis investigating seed mass, a species that had unknown mass, but belonged to a genus with relatively consistent seed masses across species, was allocated the mass class of the genus. Results for species- and genus-level mass classes had similar trends and this validated my genus-level approach. Similarly, the flowering phenology analysis classified species as biotically or abiotically pollinated based on genus and family classifications because individual species classifications were unavailable.

Table 6.1: Studies examined in the meta-analysis of graminoid and woody invader impacts.

Publication	Weed species	Vegetation community	Country
Graminoid invaders			
Christian & Wilson (1999)	<i>Agropyron cristatum</i>	Prairie	USA
Fairfax & Fensham (2000)	<i>Cenchrus ciliaris</i>	Pasture on former woodland & forest vegetation	Australia
Gremmen et al. (1998)	<i>Agrostis stolonifera</i>	Drainage line herbfields	Marion Is., sub-Antarctic
Kissling (2005)	<i>Nardus stricta</i>	Wetland	New Zealand
Lambrinos (2000)	<i>Cortaderia jubata</i>	Chaparral shrubland	USA
McArdle et al. (2004)	<i>Hyparrhenia hirta</i>	Woodland	Australia
McIntyre & Lavorel (1994)	Annual and perennial grasses	Grass-dominated vegetation (\pm <i>Eucalyptus</i> tree species)	Australia
Reed et al. (2005)	<i>Andropogon bladhii</i>	Grassland	USA
Woody invaders			
Braithwaite et al. (1989)	<i>Mimosa pigra</i>	Floodplain sedgeland, forest & ecotone system	Australia
Costello et al. (2000)	<i>Acacia sophorae</i>	Grassland	Australia
Crossman (2002)	<i>Olea europaea</i> ssp. <i>europaea</i>	Woodland	Australia
Ede (2004)	<i>Rubus fruticosus</i>	Riparian forest	Australia
Fensham et al. (1994)	<i>Lantana camara</i>	Dry rainforest & savanna woodland	Australia
Frappier et al. (2003)	<i>Rhamnus frangula</i>	Forest	USA
Holmes & Cowling (1997b)	<i>Acacia saligna</i>	Fynbos shrubland	South Africa
Leege & Murphy (2001)	<i>Pinus nigra</i>	Fore dune grassland, interdunal swale shrubland, blowout grasslands, forest edges	USA
Marchante et al. (2003)	<i>Acacia longifolia</i>	Fore dune shrubland	Portugal
Mason (unpublished data – Chapter 3)	<i>Chrysanthemoides monilifera</i> ssp. <i>rotundata</i>	Fore dune shrubland & hind dune woodland	Australia
Wearne & Morgan (2004)	<i>Cytisus scoparius</i>	Woodland	Australia
Yoshida & Oka (2004)	<i>Leucaena leucocephala</i>	Forest	Ogasawara Is., Japan

Table 6.2: Plant traits and associated descriptions used to classify species for the meta-analysis.

Plant trait	Description
<i>Vegetative traits</i>	
Growth form	Graminoids, herbs, climbers, shrubs, trees
Longevity	Short-lived: annual or biennial (life cycle completed within two years), perennial (life cycle over many years)
<i>Reproductive traits</i>	
Seed mass	Small-seeded: <1 mg; Large-seeded: >10 mg based on seed mass distributions in Westoby et al. (1992)
Flowering phenology	Asynchronous with invader (\leq half of flowering duration synchronous with invader); Synchronous with invader ($>$ half of flowering duration synchronous with invader). Species were further categorised as biotically or abiotically pollinated according to genera classifications in Renner and Ricklefs (1995) and family classifications in Ackerman (2000).

The meta-analysis procedure requires standardisation of independent studies by determining an ‘effect size’. I calculated the effect size for each comparison or study by extracting mean, standard deviation and sample size data for control (low invader abundance) and experimental (high invader abundance) groups. I used Hedge’s d metric to measure effect size, (Rosenberg et al. 2000) where:

$$d = \frac{(\bar{X}_E - \bar{X}_C)}{SD_{\text{pooled}}} J(m)$$

\bar{X}_E is the mean of the experimental or invaded group and \bar{X}_C is the mean of the control or non-invaded group. SD_{pooled} is the pooled standard deviation and is calculated as:

$$SD_{\text{pooled}} = \sqrt{\frac{(n_E - 1)(SD_E)^2 + (n_C - 1)(SD_C)^2}{n_E + n_C - 2}}$$

where SD_E and SD_C are the standard deviations of the experimental and control groups respectively and n_E and n_C are the sample sizes of the respective experimental

and control groups. $J(m)$ is a correction term that accounts for the effects of small sample sizes and is calculated as:

$$J(m) = 1 - \frac{3}{4(n_C + n_E - 2) - 1}$$

As sample size increases, the value of $J(m)$ approaches one (Gurevitch et al. 1992).

The effect size is independent of sample size and the scale of measurement used in individual experiments (Gurevitch and Hedges 1993) and is therefore a unit-free index.

A positive effect size reflected an increase while a negative effect size indicated a decrease in species richness within the plant trait classification following invasion.

Values of 0.2, 0.5 and 0.8 or greater indicated small, medium or large effects respectively (Cohen 1988). Effect sizes were then combined to provide a common estimate of the magnitude of the effect and the significance level of the overall effect was computed. Homogeneity of the effect sizes was also calculated to determine whether the effect size was common across studies (Arnqvist and Wooster 1995).

I used a mixed-effect model and assessed the contribution of woody and graminoid invaders to plant trait responses within communities using the Q statistic with a χ^2 distribution. The ratio of between-group heterogeneity (Q_B) to total heterogeneity (Q_T) was used to assess the relative contribution of an invader type to the variation in plant trait effects. A significant Q_B implied there was a difference between cumulative effect sizes for the invader types (Rosenberg et al. 2000).

While meta-analysis has considerable application in synthesising ecological studies, it has attracted controversy (Feinstein 1995, Hurlbert 2004). Here I outline steps taken to mitigate a number of potential problems associated with meta-analysis.

Invasion studies which report significant impacts are more likely to be published than those reporting equivocal results, leading to potential publication bias in the literature

(Rosenthal 1979, Gurevitch and Hedges 1993). I attempted to minimise publication bias by using studies from journals with a range of impact factors and from conference proceedings, local publications and unpublished work (Murtaugh 2002). I also manipulated databases to test hypotheses that differed from the aims of the original studies, which may further reduce publication bias. Where a number of invasion classes were reported, I used only the extreme classes to measure maximal weed impacts. Finally, the same response variable of native species richness in the defined plant trait was extracted and compared across all studies.

Considerable debate has focussed on the utility of phylogenetic corrections in comparative studies (e.g. Ricklefs 1996). Advocates of phylogenetic correction argue that without correction, phylogenetic structures within datasets result in pseudoreplication at the species level. Non independence of data inflates degrees of freedom and may produce erroneous results (Harvey and Pagel 1991, Harvey et al. 1995). In contrast, opponents of phylogenetic correction argue that its application to comparative datasets does not remove error, but prioritises one interpretation of correlative patterns over another (Westoby et al. 1995b). Consensus has not been reached in the literature, but there is agreement that while co variation among traits is correlated with phylogeny, it may also be ecologically relevant (Westoby et al. 1995a).

In this meta-analysis, I made an *a priori* division of invaders into graminoid (Poaceae) and woody classifications. This division accounted for gross phylogenetic differences among invaders. However, I have not applied quantitative phylogenetic corrections to the meta-analysis. I sought to describe patterns of invader impacts, not infer evolutionary mechanisms of invasion. It was therefore appropriate to use species as independent data points (Rees 1995). I considered that patterns of invader impacts were likely to be cross-correlated with phylogeny (Westoby et al. 1995b).

Results

H1A: *That invaders will have the strongest effect on growth forms similar to themselves:*

Woody invaders produced strong negative effects for native graminoid, herb and shrub species ($d = -1.261$, -0.827 and -1.148 respectively), a medium negative effect on vine species ($d = -0.541$) and a small negative effect on tree species ($d = -0.237$).

Although the number of studies contributing to each growth form response varied slightly, there was clear separation between confidence intervals: woody invaders suppressed graminoid and shrub more than they did tree species (Figure 6.1). In most cases, site-level meta-analyses agreed with the primary meta-analysis, however two of the four iterations for woody invader effects on native tree species revealed confidence intervals which bracketed zero ($d = -0.363 \sim -0.247$; $CI = -0.644 \sim 0.131$). This result supports my interpretation that woody invaders have only a small effect on native tree species.

Graminoid invaders also reduced native species richness within growth forms. Strong negative responses were exhibited for native graminoid, herb and vine growth forms ($d = -1.659$, -1.195 and -0.903 respectively). However, the negative effect on vines was not strongly supported in the site-level analyses with confidence intervals bracketing zero in two of the four iterations ($d = -0.954 \sim -0.759$; $CI = -2.037 \sim 0.330$). At present, therefore, there is not strong evidence for a generalised negative effect on vine species. Native shrub and tree confidence intervals bracketed zero indicating there was little evidence to suggest that graminoid invaders affected these growth forms.

I may therefore accept the hypothesis that graminoid invaders affect similar herbaceous growth forms most strongly, but I am unable to separate the effect strength of graminoid invaders on graminoid and herb species. The hypothesis is not completely accepted for woody invaders: they strongly affected functionally similar native shrub,

but not tree species. Woody invaders also strongly affected functionally dissimilar graminoid species (Figure 6.1).

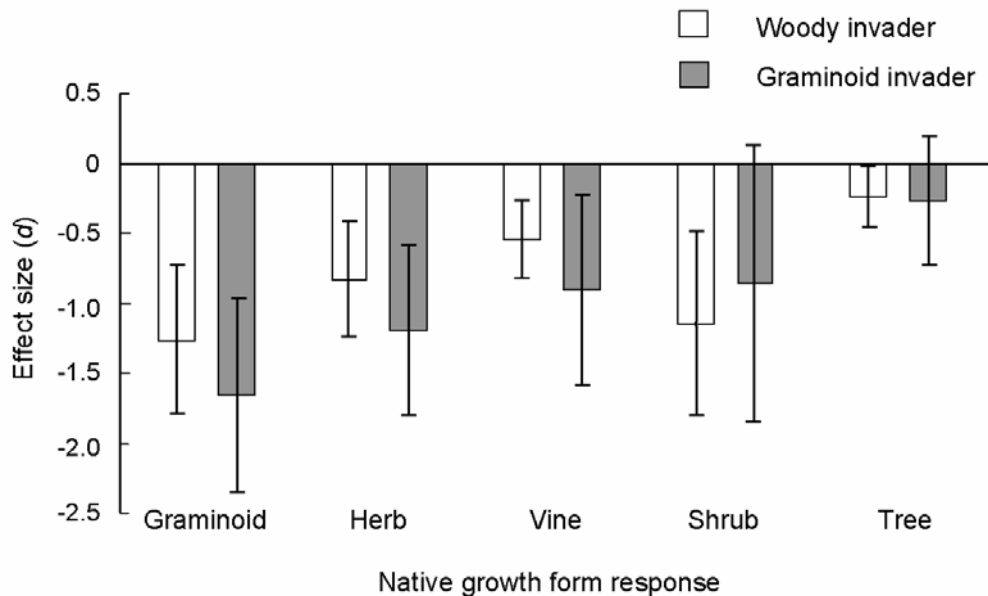


Figure 6.1: Effect size of woody and graminoid invaders on native species richness in growth form classes. Bars show means bracketed by 95% confidence intervals.

H1B: *That woody invaders will affect a wider range of growth forms than graminoid invaders:*

Woody invaders negatively affected species richness of native graminoid, herb, vine and shrub growth forms. While graminoid invaders also had negative effects on growth forms, they did not negatively affect native shrub and tree species. Their effect on vine species is unclear at present. Thus woody invaders affected a wider range of growth forms than graminoid invaders. However, within each growth form, woody and graminoid invaders had similar negative effects (Table 6.3).

Table 6.3: Q tests for primary meta-analyses with one degree of freedom for differences among cumulative effect sizes of each response variable for woody and graminoid invaders and n is the number of comparisons

Response variable	Q	P	n
Growth form			
Graminoid	0.985	0.321	27
Herb	1.170	0.279	30
Vine	1.509	0.219	22
Shrub	0.289	0.591	29
Tree	0.023	0.880	24
Longevity			
Short-lived	0.018	0.893	21
Perennial	1.301	0.254	29
Seed mass			
< 1 mg	0.197	0.657	27
> 10 mg	0.589	0.443	27

H2A: *That all longevity classes will be affected by invasion:*

Perennial species had a stronger negative response to both woody ($d = -1.514$) and graminoid ($d = -2.124$) invaders compared with the moderate negative response of short-lived species ($d = -0.615$ and -0.656 respectively) (Figure 6.2). While site-level analyses for perennial species showed a similar trend to the primary analysis, short-lived species results at the site-level indicated a less negative effect size than the primary meta-analysis and confidence intervals consistently bracketed zero for both woody ($d = -0.504 \sim -0.381$; $CI = -1.078 \sim 0.184$) and graminoid effect sizes ($d = -0.586 \sim -0.365$; $CI = -1.267 \sim 0.217$). These results imply that there may be interdependence among results for short-lived species from the primary meta-analysis and I conclude

that perennial species are more affected by both woody and graminoid invaders than short-lived species.



Figure 6.2: Effect size of woody and graminoid invaders on native species richness in longevity classes. Bars show means bracketed by 95% confidence intervals.

H2B: *That woody and graminoid invaders will have similar effects on native longevity classes:*

As I hypothesised, woody and graminoid invaders, which are mostly perennials, had similar impacts on each longevity class (Table 6.3).

H3A: *That woody and graminoid invaders will favour representation of large- relative to small-seeded species in invaded communities:*

In support of my hypothesis, graminoid invaders had less effect on large-seeded species (>10 mg) than on small-seeded species (<1 mg). The effect of graminoid invaders on the large seed mass class (> 10 mg) was small ($d = -0.372$) and confidence

intervals bracketed zero. In contrast, the effect size on the small seed mass class (<1 mg) was large ($d = -1.120$) and confidence intervals did not bracket zero (Figure 6.3).

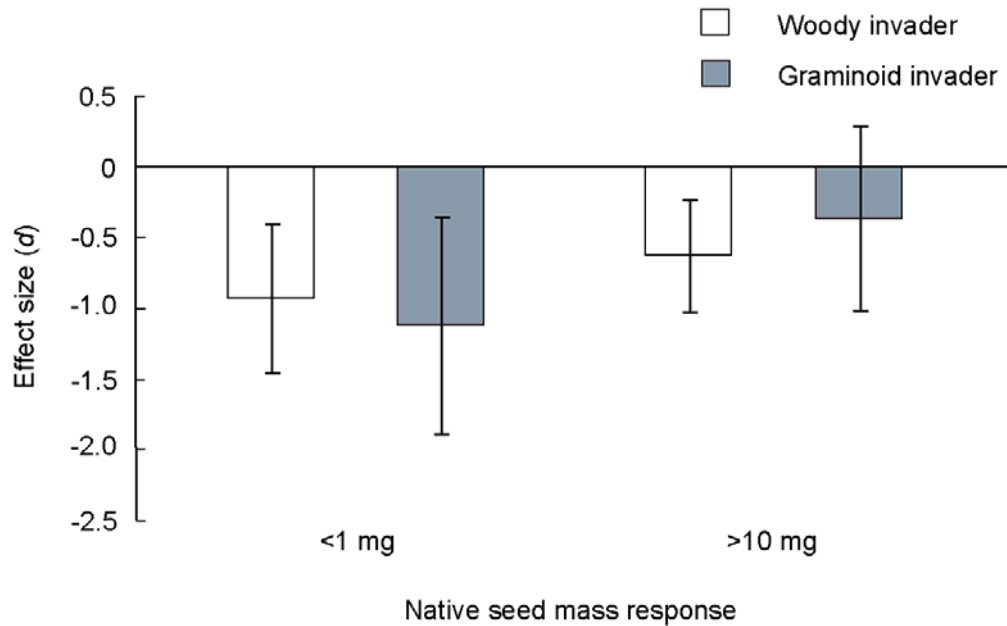


Figure 6.3: Effect size of woody and graminoid invaders on native species richness in seed mass classes. Bars show means bracketed by 95% confidence intervals.

Woody invaders had a strongly negative effect ($d = -0.933$) on small-seeded species and a moderately negative effect ($d = -0.631$) on large-seeded species. In both cases of the primary meta-analysis, confidence intervals indicated effect sizes significantly different from zero. However I am cautious about this result for large-seeded species as two of the four iterations at the site-level yielded upper confidence intervals which bracketed zero ($d = -0.822 \sim -0.504$; $CI = -1.506 \sim 0.025$) indicating woody invaders may have less of an effect on large- than small-seeded species.

H3B: *That woody invaders will have a greater impact on both large- and small-seeded species relative to graminoid invaders:*

In contrast to my hypothesis, both large- and small-seeded species had similar responses to woody and graminoid invaders (Table 6.3).

H4: *That sympatric native species whose flowering phenology is synchronous with the invader will be more affected by the invader than species whose flowering phenology is asynchronous with the invader:*

I classified native and invader species into biotic and abiotic pollination modes to isolate pollinator service effects and interspecific pollen transfer effects. In investigating pollinator service effects, I did not find any difference between native groups which were asynchronous or synchronous with the invader's flowering phenology. Both asynchronously and synchronously flowering species were strongly and negatively affected by invasion (Figure 6.4). Further meta-analyses at the site-level verified that flowering phenology was not a predictor of invader impacts, however confidence intervals for some site-level iterations bracketed zero indicating effect sizes may not be significantly different from zero (Asynchronous: $d = -1.157 \sim -0.836$ CI = $-2.402 \sim 0.530$; Synchronous: $d = -1.307 \sim -0.494$ CI = $-2.617 \sim 0.295$).

Biotically pollinated invaders were exclusively woody, but abiotically pollinated invaders consisted of graminoids and the woody invader *Pinus nigra*. When I compared the effects of biotically and abiotically pollinated invaders on native phenology classes, I found similar effects of the invader within asynchronous ($Q = 1.33$; $P = 0.25$) and synchronous ($Q = 0.01$; $P = 0.92$) classes. Further, invader effects were strongly negative for both asynchronously and synchronously flowering species (Figure 6.5). As synchronously and asynchronously flowering species had similar patterns, I concluded that the dataset did not display any interspecific pollen transfer effects for biotically or

abiotically pollinated species. Meta-analyses at the site-level supported the primary analyses with similar invader effects within asynchronous and synchronous classes, however, the strength of effect sizes was reduced with confidence intervals bracketing zero for some iterations (Asynchronous biotically pollinated: CI = -2.663 ~ 0.156; Asynchronous abiotically pollinated: CI = -2.620 ~ 0.942; Synchronous biotically pollinated: CI = -2.549 ~ 0.105; Synchronous abiotically pollinated: CI = -3.295 ~ 0.232).

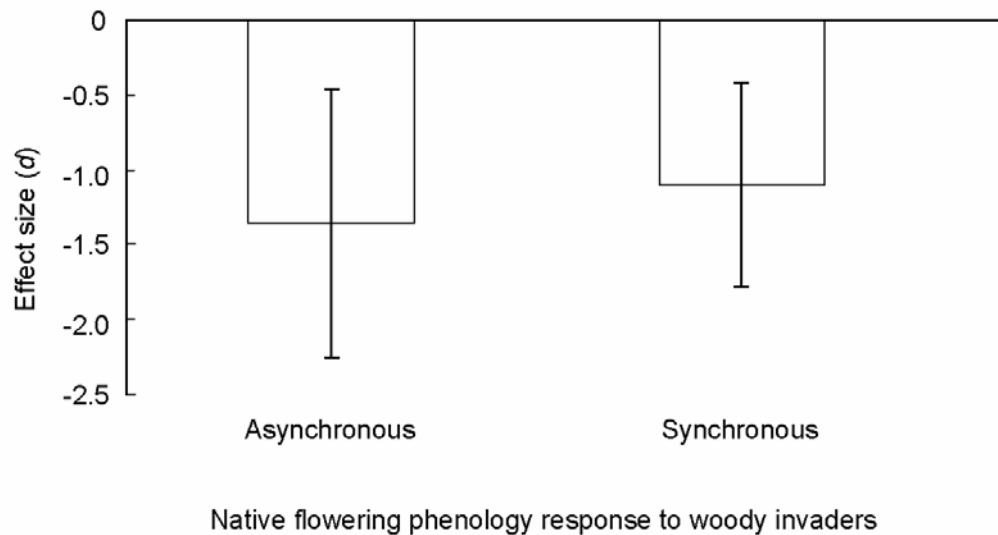


Figure 6.4: Effect size of woody invaders on native species richness in phenology classes for biotically pollinated species. Bars show means bracketed by 95% confidence intervals.

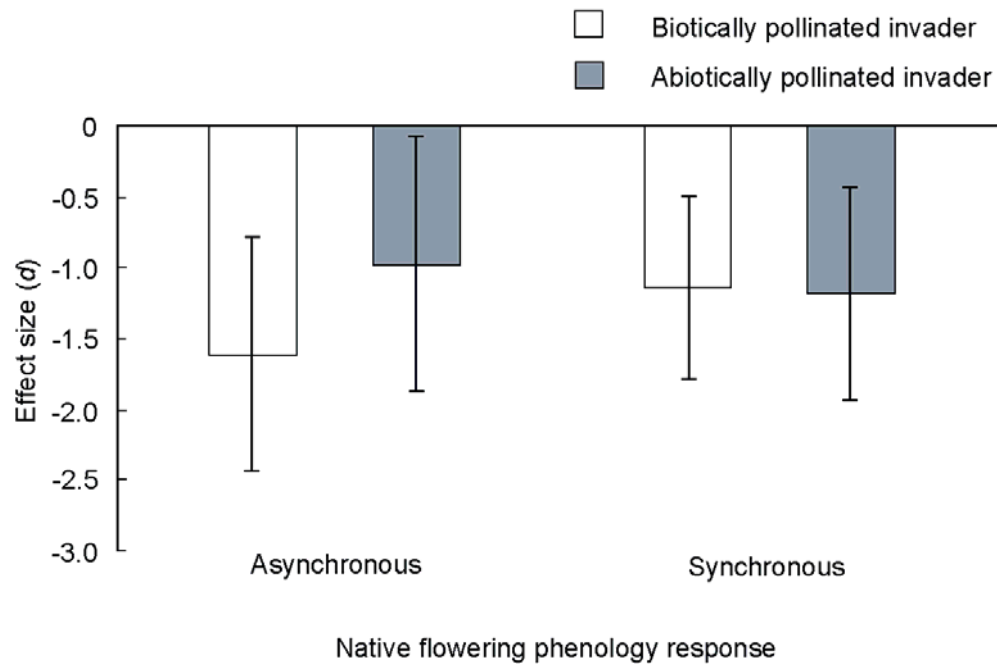


Figure 6.5: Effect size of woody and graminoid invaders on native species richness in phenology classes for biotically and abiotically pollinated species. Bars show means bracketed by 95% confidence intervals.

Discussion

Invaders as biotic filters

The study supports the widely held view that invaders have significant detrimental effects on biodiversity. The results are consistent across biomes and support the assertion that invasion is a major threat to biodiversity globally (Lovei 1997, Vitousek et al. 1997b).

However, impacts on species richness were not uniform across all plant traits, indicating that invaders may have a filtering effect on the resident community and may therefore influence community assembly. Of the trait complement represented in resident communities, graminoid invaders disproportionately affected low growing, graminoid and herbaceous growth forms, perennial strategies and small seed masses. Woody invaders disproportionately affected species with graminoid or shrub growth forms and perennial strategies. Overall, graminoid invaders had less consistent and

negative effects on growth form and seed mass plant traits than woody invaders: effect sizes for graminoid invaders were not significantly different from zero for species belonging to shrub, tree and large-seeded (> 10 mg) classes. However the meta-analysis did not reveal significant differences in effect sizes between woody and graminoid invaders across any trait classes.

Invaders had strong effects on species richness within growth forms which were similar to themselves. Graminoid invaders affected graminoid and other herbaceous native species more strongly than woody native species. Graminoid invaders may be expected to compete strongly with herbaceous native species which have similar shoot height and which similarly concentrate root biomass in the upper zones of the soil profile. Graminoid and herbaceous species therefore exploit similar light, nutrient and moisture resources. Graminoid invaders may be less effective competitors with established woody native species, especially tree species, whose roots occupy deeper sections of the soil profile (Schultz et al. 1955, D'Antonio and Vitousek 1992). My finding that graminoid invaders did not significantly affect native woody species is incongruent with other studies which have reported significant shifts in the population structure of woody species following graminoid invasion: graminoid species prevent establishment or suppress growth of native woody seedlings (e.g. D'Antonio and Vitousek 1992, Hoffmann et al. 2004, Litton et al. 2006). The meta-analysis was based on species presence information, and the persistence of woody adults following graminoid invasion may mask their long-term senescence and non-replacement in invaded communities.

Woody invaders strongly affected both native graminoid and shrub species. The large biomass and closed canopy of many woody invaders may reduce light penetration to ground level such that light becomes a limiting resource and low growth forms are

negatively affected. However, native tree species were only weakly affected by woody invaders. Established trees may tolerate invasion due to their considerable height and longevity (Lee et al. 1991): they may exploit light, moisture and nutrient resources unavailable to smaller growth forms and maintain adult representation following invasion. Despite weak invader effects on tree growth forms in my study, long-term analysis may reveal stronger effects of woody invaders if rates of tree germination and seedling growth decline under dense woody invader canopies (e.g. Fagan and Peart 2004).

Some studies in the meta-analysis reported invasion of a novel plant trait into the native community. For example, *Acacia longifolia* invasion of Portuguese dune shrublands introduced a small tree to a hitherto shrub-dominated community (Marchante et al. 2003), and *Mimosa pigra* invasion in northern Australia transformed floodplain sedgeland to tall shrubland (Braithwaite et al. 1989). Native communities may lack a particular trait due to phylogenetic constraints in the resident community or dispersal constraints from surrounding areas (Mack 2003). Assuming site factors do not preclude an invader trait, it may successfully invade and occupy hitherto unexploited niches in the community. Invasion of novel plant traits may significantly affect species composition and ecosystem processes (Mack 2003). However, invasion success may not only depend on vacant niches in the recipient community (Von Holle and Simberloff 2004). Indeed, of the traits studied in the meta-analysis, those of the invader were generally already well represented in the native communities.

Woody and graminoid invaders had similar effects on native species in different longevity classes with native perennials more negatively affected by both invader types than native short-lived species (annuals and biennials). Growth form responses indicated that native tree species were least affected by invaders, suggesting that the

perennial response was mainly attributable to species that were shrubs, climbers, herbs and graminoids. The result that perennials were most affected by invaders may reflect greater power in discerning a response for this longevity class as most databases were dominated by perennial species. However, the result may also reflect an ability by native annuals and biennials to positively respond to disturbance and gap creation. The annual strategy allows a species to exploit disturbance better than the perennial strategy (Grime 1979). Thus short-lived species, while negatively affected by the invader, may partially compensate by responding positively to the disturbance which has facilitated invasion. Negative invader and disturbance effects may compound and create a strongly negative response in native perennials. However, correlation of disturbance and invader effects in the observational datasets of the meta-analysis limits interpretation of the results.

Graminoid invaders had less impact on the large seed mass (> 10 mg) class than the small seed mass class (< 1 mg). This result may indicate that large-seeded species have a competitive advantage over small-seeded species following graminoid invasion. Large-seeded species may use metabolic reserves in the seed to tolerate shading (Westoby et al. 1992), fuel growth and thereby gain access to light resources above the graminoid invader. The primary meta-analysis indicated that woody invaders had consistently negative effects on small and large seed mass classes, however site-level meta-analyses indicated that effect sizes for large-seeded species may not be significantly different from zero. The meta-analysis has not delivered clear findings of woody weed impacts on large-seeded species. Westoby et al. (1996) found that the competitive advantage for large seeds applies only while seed reserves are deployed into the seedling and is not retained at later stages of growth. It may be that large-seeded species succeed in accessing light resources above small woody invaders but seed

reserves may be exhausted before the germinant can grow above the shade created by large woody invaders.

I found uniformly negative impacts of invaders on native species regardless of whether natives flowered asynchronously or synchronously with an invader and regardless of invader pollination mode (biotic or abiotic pollen dispersal). These results did not support the hypotheses that invader species either compete for, or facilitate, pollinator services in native species. Further, while abiotically pollinated species generally release greater quantities of pollen than biotically pollinated species (Faegri and van der Pijl 1979), my results showed similar native responses to both abiotically and biotically pollinated invaders. This result may indicate that rates of transfer for invader pollen to native stigmatic surfaces are similar regardless of pollination mode, or that transfer rates are negligible. Alternatively, invader pollen may not interfere with native pollination regimes due to low relatedness of invader and native species. While few studies have explicitly investigated the magnitude of pollen interference under natural conditions (but see de Jong et al. 1992, Ramsay and Vaughton 2000), in this study it appeared that invader flowering phenologies and pollination modes could not be used to predict effects of invasion.

Implications for restoration

The result that invaders may filter particular plant traits in a community has important implications for the design of restoration projects. Reintroduction of species belonging to poorly represented traits may be needed to reinstate structural complexity within the community. For example, I recommend restoration of perennial graminoid and herb species, along with small-seeded species as a follow-up to control of a graminoid invader, while shrub and perennial graminoid species should be targeted as a follow-up to control of a woody invader. Targeted reintroduction of species in plant

traits that are poorly represented will increase functional redundancy within the community. Functional redundancy occurs when a number of species perform equivalent functional roles: loss of one species does not result in loss of function (Walker 1992). Insurance afforded by multiple species in one functional role increases reliability (consistency of performance) of the system and resilience against further perturbation (Naeem and Li 1997, Díaz and Cabido 2001). Clearly, members of functional groups with little or no functional redundancy in invaded communities should be the focus of reintroduction programs.

Study limitations and future directions

I recognise a number of limitations of the meta-analysis. I have highlighted some discrepancies between primary and site-level meta-analysis results which may reflect interdependence among multiple sites of single invader studies. However, as discrepancies related to the magnitude of confidence intervals rather than direction of response (i.e., Q tests were consistent across primary and site-level meta-analyses), I suspect the differences are largely due to loss of power in site-level meta-analyses.

Effect sizes from comparative databases were calculated using a chronosequence approach where differences between non-invaded and invaded sites attributed to the invasion process may actually be confounded by site factors (Bakker et al. 1996). In addition, disturbance may co-vary with invasion such that effect sizes cannot be unambiguously attributed to invasion alone. Finally, dependent variables used to measure effect sizes are cross correlated (e.g. Westoby et al. 1990, Moles et al. 2005). Ultimately, causation cannot be ascertained from comparative analyses. My synthesis of multiple invader studies across a range of biomes has revealed important patterns of plant response which can be used to generate a number of hypotheses about mechanisms. For example, my growth form and longevity results indicate an interaction

between environmental constraints and internal dynamics in community assembly: light, moisture and nutrient resource competition may be strong following invasion. The relative importance of different resources may depend not only on the vegetation community, but also on the type of invader. Further, an experimental approach may clarify invader pollination dynamics. The meta-analysis did not detect disproportionate effects of the invader on synchronously flowering species over asynchronously flowering species, however, information was based on published accounts of flowering phenologies and did not incorporate potential invader-induced phenological delays (see Freeman et al. 2003 for a related discussion). Population studies connecting flowering phenology, pollinator activity, pollen limitation and seed set may be important in confirming or challenging findings of the meta-analysis. This meta-analysis has provided a springboard for a number of experimental studies: invaded communities offer a unique opportunity to test hypotheses of community assembly or disassembly because the invader biomass is readily manipulated as part of management programs.

In conclusion, the meta-analysis has highlighted a potential role of plant invaders in community assembly. Particular plant traits are disproportionately affected by graminoid and woody invaders and invasion ultimately threatens compositional integrity. The meta-analysis has also provided direction for restoration efforts and targeted species reintroduction following control of invaders.

Chapter 7

General Discussion

You become responsible, forever, for what you have tamed

Antoine De Saint-Exupéry (1962 p. 84)

Horticulture, agriculture and trade are responsible for accelerated rates of invader propagule transport. Propagule pressure then interacts with human-mediated disturbance to favour invader establishment and dominance in many natural systems. Just as humans are responsible for changing biotic and environmental parameters to favour invaders, we must also accept responsibility for understanding and managing both established and emerging plant invaders.

Understanding plant invasions

High species richness may buffer a community against disturbance and enhance productivity (Yachi and Loreau 1999, Hughes and Roughgarden 2000). Further, species composition is an important predictor of ecosystem functioning (Hooper and Vitousek 1997). My research, through a case study (Chapter 4) and meta-analysis (Chapter 6), has revealed significant negative impacts of invaders on native species richness and compositions, supporting the concept that plant invaders threaten biodiversity values both in Australian dune communities and across other biomes.

While invasion reduces native species richness and changes compositions, invaders also reduce functional redundancy (Chapter 1). Functional redundancy, where multiple species perform equivalent functional roles along an environmental gradient, may buffer a community against the effects of species loss because other members of the functional group provide compensatory roles. However, similarly to Ehrlich and

Ehrlich's (1981) rivet hypothesis, reduced redundancy will ultimately lead to a loss of function and community destabilisation. True redundancy may be difficult to demonstrate because species which are apparently functionally redundant at one scale or dimension may be functionally differentiated at another scale or higher dimension (Rosenfeld 2002). Plant traits based on attributes such as morphology have been used as surrogates for functional groups (Freitas 1999, cf. Walker and Langridge 2002), and empirical studies have shown such assumptions to be reasonable. For example, Foster and Brooks (2005) found that life form classifications adequately predicted physiological functional groups for Florida scrub. Therefore, assuming plant traits such as growth form are a surrogate for functional groupings, I found reduced functional redundancy for native fore dune graminoids, herbs and climbers and hind dune shrubs following bitou invasion (Chapter 4). I also found reduced functional redundancy of native tree species in invaded hind dune seed banks (Chapter 5). The meta-analysis revealed general trends of reduced functional redundancy following invasion. Woody invaders disproportionately adversely affected graminoid and shrub growth forms and perennial strategies over other plant traits, while graminoid invaders disproportionately adversely affected graminoid and herb growth forms, perennial strategies and small seed mass classes (Chapter 6). Thus, my research demonstrated that species loss following invasion is non random, and, despite large species pools, consistent removal of species with particular plant traits may rapidly affect community function. Reduced functional diversity may in turn facilitate future invasion (Symstad 2000, Pokorny et al. 2005).

My research has demonstrated that functional group or plant trait classifications and the redundancy concept allow greater resolution in the assessment of ecosystem status and prioritisation of conservation effort compared with the use of species richness alone. The impact of bitou invasion was imperceptible in hind dune communities when

species richness was used to compare invaded and non-invaded sites (Chapter 3).

However, categorisation of species into growth forms indicated that invaded sites had fewer shrub species than non-invaded sites (Chapter 4). Likewise, analysis of hind dune seed bank species richness indicated that invaded and non-invaded sites were similar, yet analysis of richness within growth forms revealed that invaded sites had fewer tree species represented in the seed bank than non-invaded sites (Chapter 5). Non-invaded hind dune sites therefore have greater functional redundancy than invaded sites and may exhibit greater resilience in response to disturbance (e.g. Hughes 1994). Redundancy analysis provides both a measure of ecological assessment and a focus for restoration effort, and future monitoring activities should use functional groupings in assessing invader impact and management programs.

The response of one community may not accurately predict the response of other communities to a single invader. Habitat-specific responses to plant invasion may relate to biotic variables such as species composition (Hooper et al. 2005) or abiotic variables such as structural complexity and canopy cover (Meiners et al. 2002). Few studies have actually compared the effects of a single invader in multiple habitats (Alvarez and Cushman 2002). I found that bitou more adversely affected native species richness, functional redundancy and composition as well as site-to-site variability in fore dune shrubland compared with hind dune forest communities (Chapters 3 and 4). Disparate responses to invasion in fore and hind dunes may result from different mechanisms of invasion (competition or tolerance of disturbance), duration of invasion (hind dune invasion was presumably more recent than fore dune invasion), method of introduction (bitou was deliberately planted in fore dune shrubland and progressively spread to hind dune forest) and structural complexity (hind dune vegetation has a tree canopy while fore dune vegetation has only a shrub canopy).

While the bitou case study indicated that the effects of a single invader were habitat-specific, increasing from regional to global scales provided some generalisations across invader types. Meta-analysis of 20 individual invader studies (Chapter 6) indicated that while all invaders had negative impacts on resident communities, woody invaders tended to have more consistently negative impacts (particularly on the growth form trait) than graminoid invaders. In addition, woody invaders affected shrub and herbaceous growth forms more negatively than tree and vine growth forms and perennial more than short-lived (annual and biennial) strategies. This finding by the meta-analysis complements the bitou case study where native shrub and herbaceous species respectively were significantly negatively affected by bitou invasion in hind dune and fore dune communities.

By recognising invaders as biotic filters which select for particular traits in post-invasion communities, we may improve the predictive capacity of invasion ecology. To date, much prediction has centred on attributes which make a particular species invasive (e.g. Baker 1965, Rejmánek and Richardson 1996, Lake and Leishman 2004). My results indicate that greater research effort must be directed at predicting the response of native communities to invasion because land managers must attempt to ameliorate significant impacts of extant invaders as well as monitor for potential future invaders. Meta-analysis is a powerful tool which summarises the strength of invader impacts and provides: (1) prioritisation criteria for local land managers who lack expertise or resources to evaluate appropriate species for reintroduction following control of invaders and (2) clear policy understanding of invader impacts and remediation requirements of vegetation communities.

Managing plant invasions

Control of a primary plant invader through either intensive or extensive management disturbs the resident community and may have unintended outcomes such as secondary invader establishment or primary invader reintroduction (Chapter 3). This highlights the need for ecological monitoring of management activities to ensure that project success is measured against vegetation restoration rather than administrative parameters.

I have shown that intensive, targeted management of a major woody weed, bitou, provides better ecological outcomes than extensive, non-targeted management (Chapter 3). However, intensive management has high labour demands and requires long-term commitment to site restoration. Community participation and volunteer effort are integral to the success of many ecological restoration projects (Rees and Smith 1996, Williams 2002), and intensive management may only be achieved with significant volunteer involvement. Local volunteer groups provide essential on-ground control and monitoring activities (Brown et al. 2001) and often have long term fidelity to local restoration projects (T. Mason pers. obs.). In order to effectively harness volunteer contributions to invader control and monitoring, land management agencies must recognise the importance of volunteers and co-ordinate effort, as well as encourage long-term commitment by volunteers to individual sites.

Land managers must recognise that ecological restoration requires considerable intervention. Invader control alone may be insufficient to restore reference native conditions due to loss of native species following invasion or management activities. Compounding factors such as absence from the soil seed bank (Chapter 5) and dispersal limitation (Seabloom et al. 2003b) may prevent recolonisation of native species to managed sites. While soil seed banks may be a stabilising factor for species with persistent seeds, divergence between the standing vegetation and seed bank

compositions has been recognised in many habitats (Thompson and Grime 1979, Warr et al. 1994, Holmes and Cowling 1997b), including hind dune vegetation of this study. Active reseeding or replanting following management may be required for species with transient seed banks or alternate storage modes. Managers must avoid sole reliance on soil seed banks and incorporate comprehensive and targeted replanting or reseeding activities into management planning.

Stabilisation of dune communities is an important conservation goal. These communities represent a vegetated buffer at the beach interface and are instrumental in regulating sand movement and moderating abiotic conditions (e.g. Avis and Lubke 1996) along with providing habitat for a diversity of flora and fauna, including threatened species. Invaded fore dune communities require reintroduction of graminoid, herb and climber species, while invaded hind dune communities require shrub and tree reintroduction to increase diversity and functional redundancy in the community (Chapter 3, 5). It is important to note however, that restoration efforts may be unable to reassemble the original dune community due to “humpty-dumpty” effects where local extinction of catalyst species or different sequences of species reintroduction leads to alternate communities (Pimm 1994). Hind dune communities may be less susceptible to humpty-dumpty effects and may therefore be prioritised for restoration, as diversity and richness measures are less affected compared with fore dune communities.

Management of the primary invader may assist establishment and spread of secondary invaders, incidental exotics and seedlings of the primary invader. I found that bitou-invaded fore dune sites had exotic richness values that were as low as non-invaded sites. This may indicate that bitou suppresses both exotic and native species alike. However, exotic species richness was significantly higher in intensively managed fore dune and managed hind dune sites than non-invaded sites (Chapter 3), suggesting

that bitou control released other exotic species and allowed their establishment. In addition, bitou seedling abundance was positively correlated with standing dead vegetation cover in fore dune communities (Chapter 3): increased light penetration to ground level in standing dead rather than foliated vegetation may have stimulated bitou germination. Extensively managed sites had greater standing dead vegetation than intensively managed sites and extensive management may therefore promote re-invasion by bitou. Weed propagules were present in all hind dune soil seed banks, but there was a trend of increased weed richness at managed and invaded sites compared with non-invaded sites (Chapter 5). A dilemma of weed identity emerges: is it preferable to manage a single primary invader or multiple secondary invaders? Ultimately, if management is enacted, it must be accompanied by follow up control over a number of years to eliminate weed propagules from both the standing vegetation and seed bank.

Although invasion ecologists are not social scientists, it is incumbent on them to understand the social context in which ecological research is applied (Chapter 2). Effective weed policy requires collaboration between social scientists and ecologists in directing management. Implicitly, ecologists must understand the social constraints on weed management programs. A criticism of previous weed control policy was that control actions (e.g. herbicide application) were prioritised over control outcomes (i.e., biodiversity recovery) (Williams and West 2000). Consultation between policy-makers and ecologists is particularly important in developing decision matrices for on-ground control priorities and in establishing long-term monitoring programs. For example, this study found that greater biodiversity value may be achieved through intensive management of smaller, high conservation dune areas than extensive management of larger, low conservation areas (Chapter 3). While the absolute area of treatment may be

reduced under intensive management, the sustainability of managed communities may be improved and the scale of long-term follow up may be reduced relative to extensive management approaches. It may be reasonable to extensively manage an invaded area to reduce invader biomass or propagule pressure. However, reduction of invader biomass in isolation may not achieve pre-invasion conditions when native plant traits are under-represented. Restoration must therefore augment under-represented plant traits and policy-makers must budget complete restoration costs. In all cases, policy objectives must be articulated: is invader control or community restoration the desired endpoint?

To date, monitoring and restoration budgets in Australia have been inadequate and ecologists must agitate against this politics of ignorance. A triage system across the landscape may be necessary in the medium term in order to maximise the conservation benefits of land restoration (C. Krebs pers. comm.): my research has demonstrated that hind dune sites have greater restoration potential than fore dune sites and should therefore be prioritised for conservation effort. If original species compositions cannot be attained, restoration of function and redundancy may be the next objective – utility of this approach may be determined with large-scale restoration experiments.

Future research

This study has generated a number of future potential research directions. The study highlighted the importance of reintroducing native propagules to managed and invaded communities. It is important however, to determine whether reseeded or replanting programs create viable populations of native species. In turn, as in the present study, reseeded or replanted communities should be compared with reference native communities using variables such as functional redundancy, species variability and vegetation structure along with species richness and composition to assess ecological success of restoration. Success may be measured not only using vascular plant

responses but also non-vascular bryophytes, lichen, fungi and animal community responses.

This study has demonstrated the importance of ecological monitoring of invader control programs. While this snap-shot approach provides baseline data, control programs would profit from long-term scientific monitoring which follows the restoration trajectories of communities. It may be appropriate to include a subset of sites from this study in a long-term bitou control and dune restoration monitoring program. It may also be appropriate to undertake a detailed population-level study which tracks bitou propagule pressure and its interactions with mechanical / herbicide-based and biological controls to assess which combinations of control best minimise bitou propagule pressure and seed bank accumulation. Similarly, management priorities may be informed by studies which research the response of secondary invaders to management activities: categorisation of secondary invaders as ‘weak’ or ‘strong’ based on their degree of co-existence with residents (Ortega and Pearson 2005) will determine control priorities.

An important limitation of this study is correlation of invader and disturbance effects. In both the bitou case study and meta-analysis, direct causality of native species decline cannot be conclusively attributed to invasion. Rather, disturbance and habitat modification may drive species loss with invader dominance a consequence of this process (Didham et al. 2005). Future research may utilise hypotheses generated from the meta-analysis and functional group responses illustrated in the bitou case study to devise manipulative experiments which decouple invader and disturbance effects. Research questions may include: is competition between bitou and native shrub species greater in hind dune compared with fore dune vegetation? Does this mechanism of invasion relate to a disturbance gradient? What is the limiting resource in nutrient-poor,

exposed, high-light dune vegetation? Does bitou affect resource availability? Do native plant traits have consistent responses to an invader in the presence and absence of disturbance?

Finally, cross-disciplinary research which explicitly links different policy scenarios with ecological outcomes is an important direction for future research. For example, economic modelling may clarify the ecological outcomes and human costs of different policy initiatives (Odom et al. 2003) and offers increased dimensionality and political relevance in natural resource management.

My thesis has investigated invader impacts at regional and international levels. I found that invader impacts are consistently negative, but the strength of impact is dependent on the type of invader (woody invaders have more consistently negative impacts on plant traits than graminoid invaders) and the vegetation community (bitou affects fore dune shrublands more negatively than hind dune forests). Consequently, the present strategy of prescriptive management across communities may be both ecologically ineffective and inefficient. While policy has been formulated to control the distribution and abundance of recognised invaders, I have demonstrated that invader management does not always achieve restoration of non-invaded communities. Thus, management programs must categorise invader impacts and undertake targeted restoration of invaded communities. Programs must be continually monitored and adapted for optimal biodiversity outcomes.

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