Impacts of invasive exotic plants on reptile and amphibian assemblages

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Certificate of Authorship/Originality

I certify that the work in this thesis has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree except as fully acknowledged within the text.

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Signature of Student

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Abstract

The invasive spread of exotic plants into native vegetation can pose serious threats to native faunal assemblages. This is of particular concern for reptiles and amphibians because they form a significant component of the world's vertebrate fauna, play a pivotal role in ecosystem functioning and are often neglected in biodiversity research. A framework to predict how exotic plant invasion will affect reptile and amphibian assemblages is imperative for conservation, management and the identification of research priorities.

In this thesis I present and test the first predictive framework to describe the impacts of exotic plant invasions on reptiles and amphibians. Central to the framework is the identification of exotic plant and native reptile and amphibian life-history traits that influence the response of reptiles and amphibians to exotic plant invasion. These traits are integrated into three mechanistic models based on exotic plant invasion altering: (1) habitat structure; (2) herbivory and predator-prey interactions; (3) the reproductive success of reptile and amphibian species and assemblages. With this framework, I identified novel growth forms and structural features of exotic plants and small body size of reptiles and amphibians as life-history traits most likely to be linked to strong and readily detectible impacts of invasion.

A test of framework predictions against available empirical evidence in the literature provided support for predictions from each of the three mechanisms of the framework. I performed field-work to test predictions relating to differential effects of exotic plant growth forms and the susceptibility of small-bodied native reptile and amphibian species to invasion. I compared the impacts of Lantana (*Lantana camara*), which differs strongly in growth form to the dominant native vegetation in the dry sclerophyll forest it invades, and Bitou Bush (*Chrysanthemoides monilifera* ssp. *rotundata*) which provides a similar growth form replacement in the coastal heathland it invades. Lantana significantly altered habitat structure by increasing understorey cover, creating cooler and shadier conditions. Lantana invasion was associated with lower reptile abundance, particularly of the scincid lizard *Lampropholis delicata,* the

smallest reptile species present. In contrast, Bitou Bush did not significantly alter habitat structure, insolation or habitat temperature and was not associated with significant changes in reptile abundance.

The findings of this thesis confirm the importance of plant and animal life-history traits in determining responses of reptiles and amphibians to exotic plant invasions. The trait-based approach employed in this thesis offers considerable benefits to assessing the impacts of exotic plant invasion on native biodiversity. In particular, my framework provides a basis for predicting impacts and determining future research and management priorities.

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Acronyms & Abbreviations

ANOSIM	Analysis of Similarity
ANOVA	Analysis of Variance
C	Carbon
CI	Confidence Interval
DBH	Diameter at Breast Height
ESD	Environmental Sex Determination
EST	Eastern Standard Time
GLM	General Linear Model
GenLMM	Generalised Linear Model
GLMM	Generalised Linear Mixed Model
GSD	Genotypic Sex Determination
HSD	Honestly Significant Difference
LSD	Least Significant Difference
M-BARCI	Multiple Before-After Reference Control-Impact
PAR	Photosynthetically Active Radiation
N	Nitrogen
nMDS	Non-metric Multidimensional Scaling
NSW	New South Wales
P	Phosphorus
SE	Standard Error
SL	Shell Length
SVL	Snout-Vent Length
TL	Total Length
TSD	Temperature-dependent Sex determination
UV	Ultraviolet

Chapter 1: General introduction

1.1 Biological invasions

The introduction of non-native or 'exotic' species into new regions can have substantial impacts on native biota and ecosystems (Elton, 1958; Usher, 1988; Blossey, 1999; Vilá *et al*., 2011). While introductions of exotic species may occur as a result of natural phenomena, the rate and scope of introductions has been greatly increased by humans (Vitousek *et al*., 1997; Richardson & Pyšek, 2006; Simberloff *et al*., 2013). Such introductions have become sufficiently frequent and widespread to threaten biodiversity on a global scale (IUCN, 2000; Sax & Gaines, 2003; Millennium Ecosystem Assessment, 2005). Indeed, the spread of exotic species is recognised as a major source of global environmental change (Vitousek *et al*., 1997; Ricciardi, 2007; Tylianakis *et al.,* 2008) and has been ranked as second only to habitat loss as a threat to biodiversity (Wilcove *et al*., 1998; Gurevitch & Padilla, 2004).

Studies of biological invasions have focused on the traits of successful invasive species (Sakai *et al*., 2001; Pyšek & Richardson, 2007; Phillips *et al*., 2010), attributes of invasion prone ecosystems (Davis *et al*., 2000), the impacts of invasion by exotic plants or animals on native biota and recipient ecosystems (Parker *et al*., 1999; Levine *et al*., 2003; Hejda *et al*., 2009) and the interactions among these factors (Vermeij, 1996; Fritts & Rodda, 1998; Mack *et al*., 2000; Sax & Brown, 2000). Surprisingly, despite a large body of work in the field of invasion ecology, we know much less than would be expected about the ecological impacts of exotic plant species on native fauna (Murray *et al*. 2007). In particular, there is a paucity of information concerning the mechanisms underpinning variation among exotic plant species in their ecological impacts on fauna.

Recently, there has been vigorous debate about the merits of current approaches to the study and management of the ecological impacts of biological invasions. It has been argued that a focus on the 'exotic' origins of non-native species is counter-productive and that priorities should be based on whether species produce harmful or beneficial effects irrespective of their origin (Davis *et al*., 2011; Thompson & Davis, 2011). In contrast, it has been argued that most ecologists and management

authorities are chiefly concerned with the subset of non-native species that harm or threaten native biota and ecosystems (Simberloff *et al*., 2011; Lockwood *et al*., 2011). This debate is made difficult simply by the fact that determining whether species are harmful or beneficial is by no means straightforward. Some non-native species may produce both harmful and beneficial effects, while the harmful impacts of others may not be apparent until many years after their introduction (Simberloff *et al*., 2011) or be difficult to detect (Hulme *et al*., 2011; Simberloff *et al*., 2013). It is increasingly clear from this debate that an enhanced ability to predict and understand the impacts of biological invasions would be highly beneficial. However, general models for predicting and understanding the impacts of invasions remain elusive. A related issue is the need to predict the response of native species and ecosystems to control or removal of exotic species. Restoration of pre-invasion ecological communities may not always be possible or even desirable as exotic species often establish complex interactions with native biota, interactions that if lost will potentially be harmful to native fauna (Vermeij, 1996).

1.2 Exotic plant invasions

The deliberate and accidental introduction of exotic plants to areas beyond their natural dispersal potential is a major source of biological invasions (Heywood, 1989; Blossey, 1999; Lonsdale, 1999; Levine e*t al*., 2002; Richardson & Pyšek, 2006). Exotic plant species transported to new areas may become 'naturalised' and establish self-sustaining populations (Richardson *et al*., 2000). Exotic plant invasions occur when naturalised species spread to areas distant from their introduction sites and establish populations (Richardson *et al*., 2000). Exotic plant invasions have occurred in most environments throughout the world (Usher, 1988; Lonsdale, 1999), even including remote sub-Antarctic Islands (Smith, 1996; Frenot *et al*., 2005). The impacts of these invasions include alteration of native plant communities (Vitousek & Walker, 1989; Adair & Groves, 1998; Levine *et al*., 2003; Hejda *et al*., 2009; Mason *et al*., 2009), changes to abundance, richness and composition of invertebrate communities (Slobodchikoff & Doyen, 1977; Griffin *et al*., 1989; Herrera & Dudley, 2003;

Greenwood, *et al*., 2004; Ernst & Cappuccino, 2005; Robson *et al*., 2009), impacts on soil microbes (Yu *et al*., 2005; Li *et al*., 2006) and changes to ecosystem structure and function (Mack & D'Antonio, 1998; Levine *et al*., 2002; Ehrenfeld, 2003; Brooks *et al*., 2004; Standish *et al*., 2004; Strayer *et al*., 2006; Gerber *et al*., 2008).

Australia has experienced a high rate of exotic plant introductions with approximately 27,000 plant species introduced since European settlement in 1788 (Randall, 2007). Over 2,700 of these exotic plant species have become naturalised and now comprise 10 to 15% of total plant species in Australia (Groves, 2002; Randall, 2007). More than 130 of these naturalised species have become invasive (Randall, 2007). As a result many Australian ecosystems have been affected by exotic plant invasions (Adair & Groves, 1998) and the ecological impacts of many of these invasions have been severe (Adair & Groves, 1998; Groves, 2002). For example, invasive exotic plant species are second only to land clearing as a threat to biodiversity in the state of New South Wales (Coutts-Smith & Downey, 2006). Managing these impacts places substantial burdens on public resources with at least AU$19.6 million spent each year in Australia on controlling exotic plants invading natural environments (Sinden *et al*., 2005). Less tangible costs include loss of ecosystem services due to the effects of exotic plant invasions into natural ecosystems and the opportunity costs of volunteer labour to manage weeds that could be otherwise employed (Sinden *et al*., 2005).

1.3 Impacts of invasive exotic plants on vertebrates

The wide range of exotic plant impacts observed on plants, invertebrates, ecological communities and ecosystem function has prompted scientific and public concern about the effects of invasive exotic plants on vertebrates. Some of these concerns have been speculative in nature (Hinchcliffe, 1977); however, there is a growing body of evidence to indicate that exotic plant invasions can have significant impacts on vertebrates (Mazotti *et al*., 1981; Braithwaite *et al.*, 1989; Ellis *et al*., 1997; Fleishman *et al*., 2003; Isacch *et al*., 2005). These impacts may be complex and there is no consistent pattern of positive, negative or neutral effects (Murray *et al*., 2007). Of those exotic plants that become naturalised and invasive only a sub-set are known to

exert impacts on vertebrates (Coutts-Smith & Downey, 2006). Furthermore, individual plant species may exert idiosyncratic effects on various taxa. For example, invasion of the exotic shrub *Mimosa pigra* into native sedgeland in Northern Australia reduced abundances of birds and reptiles, however frog abundance was unaffected and abundance of the red-cheeked dunnart (*Sminthopsis virginiae*) increased (Braithwaite *et al.*, 1989). Effects may even vary within taxa. Invasion of the exotic tree *Tamarix aphylla* in central Australia has been associated with reduced abundance of most bird species, unchanged abundance of granivorous birds and increased abundance of some insectivorous birds (Griffin *et al*., 1989; Groves & Willis, 1999).

The variable nature of invasive exotic plant impacts on vertebrates raises important questions. In particular, are there any plant life-history traits such as growth form or structure that make some exotic plants more likely to exert significant impacts than others? Equally, are there particular animal life-history traits such as body size, diet or reproductive mode that render some native animal species more sensitive to these influences and how might these plant and animal traits interact to determine the magnitude and scope of impacts? Identifying such plant and animal traits, and interactions between, them would offer considerable benefits in predicting the impacts of exotic plant invasions and developing management priorities. To date, however, the lack of consistent trends in vertebrate responses to exotic plant invasion has made identification of such traits difficult. This is particularly the case for reptiles and amphibians where a paucity of empirical studies (when compared with other taxa) further complicates any attempt to identify general trends.

1.4 Importance of reptiles and amphibians to biodiversity

Reptiles and amphibians are major components of biodiversity and perform important roles in many ecosystems (Gardner, 2001; Pough *et al*., 2004). However, reptile and amphibian species and populations are under unprecedented threat. Declines and extinctions of amphibian species are occurring on a global scale (Alford & Richards, 1999; Beebee & Griffiths, 2005; Wells, 2007). Approximately a third of all amphibian species have declined or become extinct (Stuart *et al.,* 2004). Approximately 4% of

local reptile populations have become extinct worldwide since 1975 (Sinervo *et al*., 2010). By 2080 local reptile population extinctions are predicted to reach 39% worldwide and reptile species extinctions to reach 20% worldwide (Sinervo *et al*., 2010). Causes of reptile and amphibian decline include habitat destruction, climate change, pathogens, increased ultraviolet radiation and biological invasions (Alford & Richards, 1999; Beebee & Griffiths, 2005; Sinervo *et al*., 2010). While many of these causes have been the focus of considerable research effort, there remains a paucity of studies documenting the impacts on reptiles and amphibians of biological invasions in general and invasive exotic plants in particular.

Reptiles and amphibians are of particular ecological importance in Australia which possesses perhaps the world's most diverse and abundant herpetofauna. Over 900 reptile species (Wilson & Swan, 2010) and 200 amphibian species (Tyler & Knight, 2011) have been described to date. The true number of species present is almost certainly higher with previously cryptic species being described on an ongoing basis. Threats to the reptiles and amphibians in Australia thus imperil biodiversity at local, continental and global scales. The abundance and diversity of reptiles and amphibians, coupled with a high rate of exotic plant introductions means that Australia provides unique opportunities for developing and testing models that predict how invasive exotic plant traits interact with those of native reptiles and amphibians to determine impacts. Furthermore, the importance of reptiles and amphibians to Australian biodiversity makes such research a high priority. At least 21 Australian reptile and amphibian species are threatened with extinction by exotic plants (DEWHA, 2009). This does not include species whose abundance may have been altered by exotic plant invasions but which are not currently classified as threatened.

1.5 Research significance and objectives

In this thesis I propose and empirically test the first framework for predicting the impacts of exotic plant invasions on reptiles and amphibians. A central feature of the framework is the identification of how exotic plant and native animal life-history traits interact to determine impacts. While previous studies have been vital in furthering our

understanding of exotic plant traits linked to invasive success (e.g. Sakai *et al*., 2001; Pyšek & Richardson, 2007; Phillips *et al*., 2010) and impacts of invasions on reptiles and amphibians (e.g. Braithwaite *et al.*, 1989; Griffin *et al*., 1989; Sax, 2002; Valentine, 2006; Garden *et al*., 2007), there is scope to develop research that identifies interactions between exotic plant and native animal traits within a predictive framework.

The predictive framework presented in this thesis is built upon ecological theory and established knowledge of exotic plant impacts. Model predictions are tested both by reviewing empirical evidence available from published literature and field investigations of the impacts of exotic plants on reptile and amphibian assemblages. It is not feasible to conduct field-based tests of all model predictions in the course of a single research project. I therefore concentrate on several key predictions pertaining to the importance of exotic plant growth form and body size and diet of native reptiles and amphibians. Opportunities for further work to test remaining model predictions are identified and a range of possible approaches proposed. The work presented here and further testing of predictions will provide a basis for informing and prioritising environmental management and exotic plant control efforts.

In developing the fieldwork component of this research, I identified a significant ethical issue regarding marking and individual recognition of amphibians. In particular, the need to develop less invasive alternatives to current marking techniques such as toe-clipping and implanted marks for studies where only short-term mark retention is required. To address this issue I conducted a laboratory trial of minimally-invasive skin staining methods for marking amphibians.

1.6 Thesis objectives

There are five objectives addressed in this thesis:

1. To identify invasive exotic plant and native reptile and amphibian life-history traits that influence the response of reptiles and amphibians to exotic plant invasion.

2. To develop a framework that describes how these plant and animal life-history traits interact to determine the magnitude and scope of impacts of exotic plant invasions.
3. To test model predictions against currently available empirical evidence in the literature.
4. To test key model predictions through field investigation of the impacts of invasive exotic plants on reptile and amphibian assemblages.
5. To investigate minimally-invasive methods of marking amphibians for short-term studies.

1.7 Thesis structure

The objectives of this thesis are addressed in the following manner:

Chapter 2 presents a predictive framework that integrates three mechanistic models of how the life-history traits of invasive exotic plants interact with those of native reptiles and amphibians to determine impacts. These models are based on exotic plant invasion altering: (1) habitat structure; (2) herbivory and predator-prey interactions; (3) the reproductive success of reptile and amphibian species and assemblages. I provide a series of testable predictions from these models that arise from the interplay over time among three exotic plant traits (growth form, area of coverage, taxonomic distinctiveness) and six traits of reptiles and amphibians (body size, lifespan, home range size, habitat specialisation, diet, reproductive strategy). I present evidence from the scientific literature to support predictions from each of the three model mechanisms. This chapter has been published as a peer-reviewed manuscript: Martin, L.J. & Murray, B.R. (2011) A predictive framework and review of the ecological impacts of exotic plant invasions on reptiles and amphibians. *Biological Reviews* 86, 407-419.

In Chapter 3 I present the results of fieldwork to test several key model predictions. In particular, the importance of exotic plant growth form and reptile body size in determining the nature and magnitude of exotic plant impacts. I investigated the response of native reptiles to invasion by Lantana (*Lantana camara*) which differs strongly in growth form to the dominant native vegetation in the dry sclerophyll forest

it invades and Bitou Bush (*Chrysanthemoides monilifera* ssp. *rotundata*) which provides a similar growth form replacement in the coastal heathland it invades. I utilised a multi-site comparison approach to study the effects of both exotic plant species with care taken to ensure comparability between invaded and uninvaded sites. The key findings of this chapter were presented as a spoken paper: Martin, L.J. & Murray, B.R. (2011) "How do native reptile assemblages respond to invasion by exotic plant species of differing growth form?" at the 2011 Ecological Society of Australia annual conference.

Chapter 4 presents a case study of the response of a native reptile assemblage to exotic plant control. I employed a multiple before-after reference control-impact (M-BARCI) design to examine the responses of reptiles to control of invasive Bitou Bush *Chrysanthemoides monilifera* ssp. *rotundata* with glyphosate herbicide. This chapter has been published as a peer-reviewed manuscript, Martin, L.J. & Murray, B.R. (2013) A preliminary assessment of the response of a native reptile assemblage to spot-spraying invasive Bitou Bush with glyphosate herbicide. *Ecological Management and Restoration* 14, 59-62.

In Chapter 5 I present the results of multi-site comparisons to examine the differing effects of Lantana and Bitou Bush on habitat structure and heterogeneity. I examine and compare the effects of these two exotic plant species on habitat structure, leaf litter composition and depth, availability of light and leaf litter temperature; factors with the potential to exert significant influences on the suitability of habitat for reptiles and amphibians. I interpret the results of Chapter 3 in light of these findings.

In Chapter 6 I again utilise multi-site comparisons to determine whether the responses of reptiles to invasion by Lantana and Bitou Bush may be attributed to variations in abundance and composition of invertebrate prey between invaded and uninvaded sites. I also interpret the results of Chapter 3 in light of these findings.

Chapter 7 presents the results of a laboratory experiment to test novel skin-staining techniques for minimally-invasive short-term marking of amphibians. This chapter has been published as a peer-reviewed manuscript Martin, L.J. & Murray, B.R.

(2011) A comparison of short-term marking methods for small frogs using a model species, the striped marsh frog (*Limnodynastes peronii*). *Herpetological Journal* 21, 271-273.

In Chapter 8, the final chapter, I assess whether the aims of this thesis were met. I interpret the overall findings of each chapter and the extent to which predictions of the Chapter 2 framework have been supported by empirical evidence. I also consider the management implications arising from this thesis and provide recommendations for further research.

Chapter 2: A predictive framework and review of the ecological impacts of exotic plant invasions on reptiles and amphibians.

2.1 Introduction

The introduction of exotic species into new regions and ecological systems poses a serious threat to biodiversity (IUCN, 2000; Millennium Ecosystem Assessment, 2005). Plant assemblages infiltrated by exotic plants often experience declines in native species richness, diversity and functioning (Braithwaite *et al*., 1989; Griffin *et al*., 1989; D'Antonio & Vitousek, 1992; Gordon, 1998; Parker *et al*., 1999; Clarke *et al*., 2004). As a consequence, the establishment and invasive spread of exotic plants in native vegetation presents major challenges for the management and conservation of biodiversity.

The effects of exotic plant invasions on native plant communities have been the focus of considerable research efforts around the world. The majority of ecological impacts identified include reductions in native plant species richness and alterations to ecological function (Vitousek & Walker, 1989; Adair & Groves, 1998; Levine *et al*., 2003; Ogle, *et al*., 2003; Vila *et al*., 2006; Hejda *et al*., 2009). Sometimes, however, the diversity of plant assemblages invaded by exotic plants may be unchanged, or even show signs of increase (Sax & Gaines, 2003; Sax *et al*., 2005). Thus, invasion of native vegetation by exotic plants does not always lead to declines in native plant communities, which has important implications for the resident native animal species and assemblages.

The arrival of exotic plants in new ecosystems can affect native animal species and assemblages by modifying vegetation composition and structure. There is a growing body of research demonstrating that the incursion of exotic plants into native vegetation causes significant alterations to species richness, composition and abundance of invertebrates (Slobodchikoff & Doyen, 1977; Griffin *et al*., 1989; Herrera & Dudley, 2003; Greenwood, *et al*., 2004; Ernst & Cappuccino, 2005; Robson *et al*., 2009). Possible mechanisms underpinning the impacts of exotic plants on invertebrate assemblages include reduced habitat complexity and unsuitability of introduced plants

to native herbivores (Slobodchikoff & Doyen, 1977; Herrera & Dudley, 2003; Ernst & Cappuccino, 2005). Like native plant assemblages, the ecological outcomes of exotic plant invasion on invertebrate communities are quite varied. As yet, however, there is no general model that can account for the range of impacts observed in invertebrate communities (but see Sax *et al*., 2005; Murray *et al*., 2009).

The presence of exotic plants in native plant assemblages can have significant effects on native vertebrate inhabitants. For example, Mazzotti *et al*. (1981) observed reduced abundance of three native mammal species in areas of Southern Florida (USA) occupied by the exotic trees *Melaleuca quinquenervia* and *Casuarina equisetifolia*. Despite concern, however, that exotic plant invasion will cause decline of native bird and mammal species, the current literature reveals no consistent positive, negative or neutral effects of increases in exotic plant cover within mammalian and avian assemblages (Murray *et al*., 2007). Furthermore, there is a conspicuous absence of a general understanding of the impacts of exotic plant invasion on reptiles and amphibians, a significant component of the world's vertebrate fauna. Given the pivotal roles of reptiles and amphibians in the functioning of ecosystems (Burton & Likens, 1975; Gardner, 2001; Pough *et al*., 2004), as well as the importance of amphibians as key bioindicators of ecosystem change and biodiversity loss (Blaustein & Wake, 1990; Vitt *et al*., 1990; Halliday & Heyer, 1997; Gardner, 2001), this issue warrants critical attention.

Here, I present a framework that predicts how reptile and amphibian species and assemblages respond to invasion of their native habitats by exotic plant species. The framework integrates three mechanistic models, each linked to a set of testable predictions. Central to the models are the traits of the invading plant species (growth form, area of coverage, taxonomic distinctiveness), variation in reptile and amphibian life-history traits (body size, lifespan, home range size, habitat specialisation, diet, reproductive strategy) and interactions between these plant and animal traits. A key component of the framework is the explicit inclusion of the timeframe for the effects of exotic plant invasion to become detectable. This temporal element recognises that there may be a lag time before ecological effects are discernible. I also provide a

comprehensive review of published empirical studies of the impacts of exotic plants on reptiles and amphibians. The aim of this chapter is to link empirical evidence to model predictions of the framework.

2.2 Conceptual framework and mechanisms of impact

Animals must feed, avoid predation, tolerate or avoid abiotic stresses and reproduce (Anderson, 2007). The extent to which exotic plants affect reptiles and amphibians is determined by the influences they exert on these basic functions. My conceptual framework considers how exotic plant and native animal traits interact to affect these functions through three mechanistic models. The models are based on exotic plant invasion altering: (1) habitat structure, quality and heterogeneity; (2) herbivory and predator-prey interactions; and (3) the reproductive success of reptile and amphibian species and assemblages (Fig. 2.1). How these mechanisms, which are not mutually exclusive, exert an influence on reptile and amphibian species and assemblages is directly controlled by interactions between the life-history traits of exotic plants and reptiles and amphibians. For each model, I present ecological theory that shapes its basic structure, provide a series of testable predictions and describe empirical evidence based on a literature review (Table 2.1).

There are often significant, negative ecological effects of exotic plants on reptiles, with a couple of exceptions (Table 2.1). The lack of studies on amphibians is noteworthy. As a case study for the Australian continent, I also provide lists of threatened species of Australian reptiles and amphibians identified as at risk from exotic plant invasion (Tables 2.2, 2.3). These lists indicate possible impacts of exotic plants on individual reptile and amphibian species and are often based on subjective assessments of experienced scientists and application of the precautionary principle (Coutts-Smith & Downey, 2006). Exotic plants do not necessarily represent the sole threats to these species or reasons for their decline. Thus, exotic plant invasion will, in most cases, act in concert with other threats and environmental stresses.

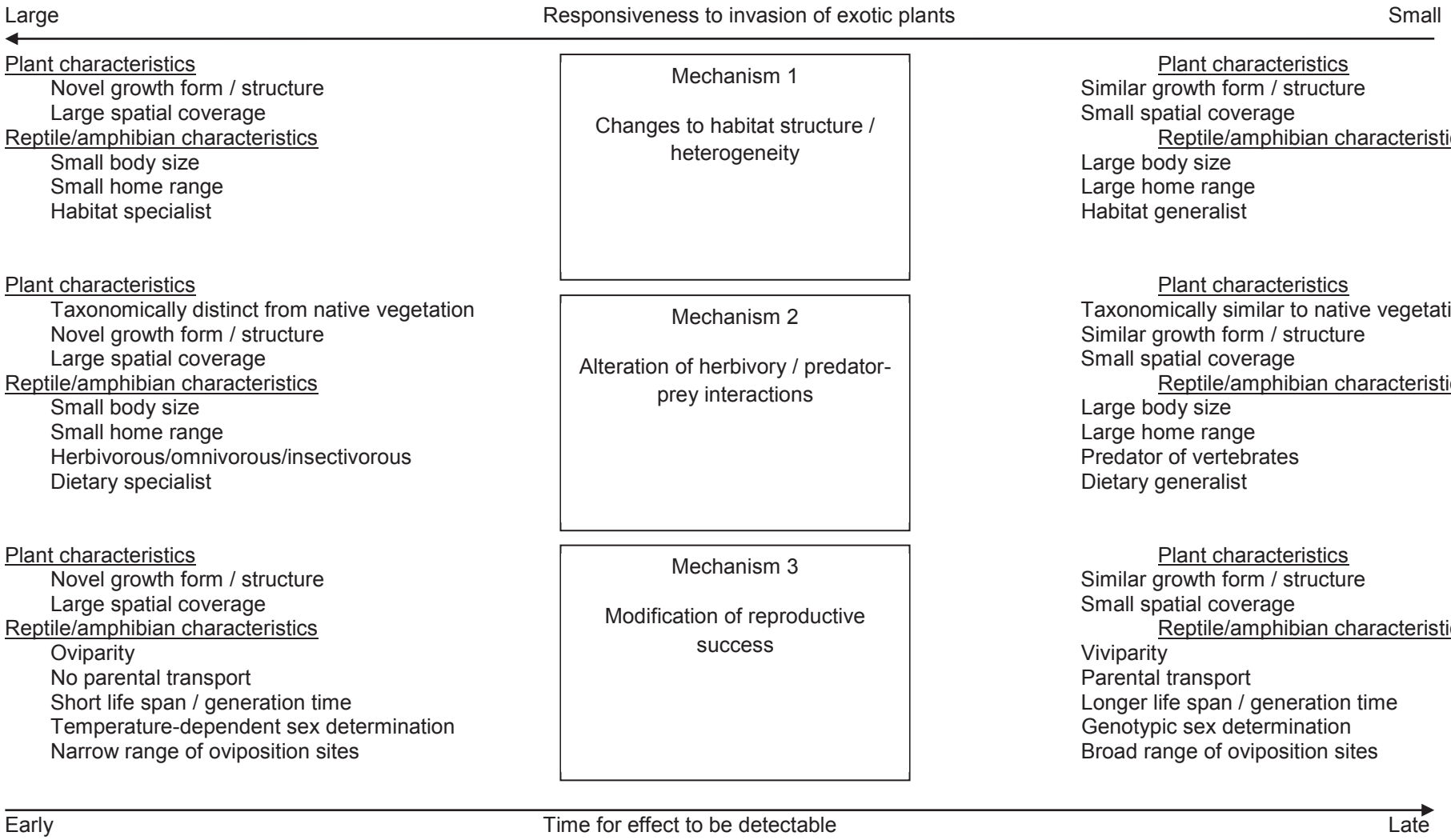

Fig. 2.1. Three mechanisms determining the impacts of exotic plants on reptiles and amphibians and the role of plant and reptile/amphibian traits. Intensity of response to invasion increases from right to left in relation to plant and reptile/amphibian traits (top arrow). The timeframe for detectable impacts increases from left to right (bottom arrow).

Table 2.1. Studies examining the ecological impacts of exotic plants on reptiles and amphibians. Ecological measures include species richness or abundance. Effect indicates the change in species richness or abundance (+ = increase in abundance or richness, - = decrease, 0 = no change).

Taxa	Measure	Effect	Source
All reptile species	abundance	-	Braithwaite *et al*. (1989)
All amphibian species	abundance	0	Braithwaite *et al*. (1989)
Carlia tetradactyla (lizard)	abundance	+	Fischer *et al*. (2003)
All reptile species	abundance	+	Garden *et al*. (2007)
All lizard species	abundance	-	Griffin *et al*. (1989)
All reptile species	richness	-	Hadden & Westbroke (1996)
All amphibian species	richness	0	Hadden & Westbroke (1996)
All lizard species	richness	-	Jellinek *et al*. (2004)
All amphibian species	richness	0	Sax (2002)
Scincid lizards	richness	-	Smith *et al*. (1996)
All lizard species	abundance	-	Valentine (2006)

2.2.1 Model 1: changes to habitat structure, quality and heterogeneity

(*a*) *Theory*

Habitat structure and spatial heterogeneity are important factors regulating the characteristics of reptile assemblages (Pianka, 1967). Changes in habitat features correspond with changes in the composition and structure of reptilian assemblages (Heatwole & Taylor, 1987). Typically, more diverse vegetation or increased structural diversity increases the number of spatial niches available, which leads to increased reptile species richness (Heatwole & Taylor, 1987). Spatial heterogeneity is also an important influence on within-habitat diversity of amphibians for similar reasons (Duellman & Trueb, 1994). Changes to vegetation and habitat structure from exotic plant invasion will, thus, alter the availability of spatial niches and the suitability of habitat for individual species. The extent to which alteration of spatial niches will affect

Table 2.2. Australian reptile species identified as threatened by exotic plants. Selected reptile traits (native habitat, size, reproductive strategy and diet) and the threatening plant species are listed. SL = shell length; SVL = snout-vent length; TL = total length; Generic = general threat from exotic plants with no particular exotic plant species identified. Sources include Cogger (2000), Coutts-Smith & Downey (2006), Department of Environment and Climate Change (2009), Department of Environment, Water, Heritage and the Arts (2009) and Wilson & Swan (2010).

Family	Species	Native habitat	Average body size (mm)	Oviparous (O) / viviparous (V)	Diet	Threatening exotic plants
Agamidae	Grassland earless dragon (*Tympanocryptis pinguicolla*)	Temperate grasslands	50 (SVL)	O	Small invertebrates	Generic
Chelidae	Mary River turtle (*Elusor macris*)	Flowing, well-oxygenated sections of streams	400 (SL)	O	Aquatic macrophytes, aquatic insect larvae, some terrestrial vegetation	Para grass (*Urochloa mutica*), lantana (*Lantana camara*), thistles (Asteraceae), couch grass (*Cynodon* sp.)

	Fitzroy River turtle (*Rheodytes leukops)*	Flowing, well-oxygenated sections of streams	250 (SL)	O	Aquatic macrophytes, aquatic insect larvae, some terrestrial vegetation	Generic
Elapidae	Dunmall's snake (*Furina dunmalli*)	Eucalypt and *Callitris* woodland, brigalow scrub	600 (TL)	Unknown, possibly O[1]	Small scincid and gekkonid lizards	Generic
	Little whip snake (*Suta flagellum*)	Beneath rocks and logs in woodland and grasslands	400 (TL)	V	Small scincid lizards and frogs	Generic
Gekkonidae	Lord Howe Island gecko (*Christinus guentheri*)	Trees, boulder slopes and rock faces	80 (SVL)	O	Small insects and arthropods, nectar of selected tree species	Generic
Pygopodidae	Pink-tailed worm lizard (*Aprasia parapulchella*)	Beneath rocks on grassy streamside slopes in woodland	140 (SVL)	O	Ant eggs and larvae	Generic

	Marble-faced delma (*Delma australis*)	Beneath rocks and logs and in Spinifex (*Triodia* spp.) in arid areas	80 (SVL)	O	Selected arthropods, especially lepidopteran larvae	Generic
	Striped legless lizard (*Delma impar*)	Beneath rocks, logs and debris in forest and woodland habitats	90 (SVL)	O	Selected arthropods, especially lepidopteran larvae	Generic
Scincidiae	Five-clawed worm-skink (*Anomalopus mackayi*)	Beneath rocks and fallen timber in dry schlerophyll forest, eucalypt and *Callitris* woodland	100 (SVL)	O	Unknown	Coolatai grass (*Hyparrhenia hirta*)
	Leopard ctenotus (*Ctenotus pantherinus ocellifer*)	Porcupine grasses in sandy and desert habitats	90 (SVL)	O	Small insects	Generic

Lord Howe Island skink (*Cyclodina lichenigera*)	Beneath rocks, boulders and fallen timber	80 (SVL)	O	Small invertebrates	Generic
Mallee slender bluetongue (*Cyclodomorphus melanops elongata*)	Spinifex (*Triodia* spp.) grasslands, arid scrubs and heaths	130 (SVL)	V	Invertebrates, flowers, fleshy leaves and fruit	Generic
Blue Mountains water skink (*Eulamprus leuraensis*)	Riparian and swampy areas in montane forests	80 (SVL)	V	Insects, some evidence of omnivory	Generic
Nangur spiny skink (*Nangura spinosa*)	Creek banks in seasonally dry rainforest	100 (SVL)	V	Invertebrates	Lantana (*Lantana camara*)

[1] Based on closest taxonomically related species.

Table 2.3. Australian amphibian species identified as threatened by exotic plants. Selected amphibian traits (native habitat, size, parental transport and diet) and the threatening plant species are listed. Generic = general threat from exotic plants with no particular plant species identified. Sources include Cogger (2000), Coutts-Smith & Downey (2006), Department of Environment and Climate Change (2009) and Department of Environment Water Heritage and the Arts (2009).

Family	Species	Native habitat	Average body size (mm)	Parental transport	Diet	Threatening exotic plants
Hylidae	Green and golden bell frog (*Litoria aurea*)	Vegetation within or at the edges of permanent water	85	No	Small frogs	Generic
	Booroolong frog (*Litoria booroolongensis*)	Beneath boulders and debris of permanent mountain streams	45	N	Unknown	Willows (*Salix* spp.)
	Spotted tree frog (*Litoria spenceri*)	Among boulders, debris and fringing vegetation of permanent mountain streams	45	No	Insects	Blackberry (*Rubus fructicosus*)

Myobatrachidae	Giant burrowing frog (*Heleioporus australiacus*)	Burrows near water in sandy soil areas with native vegetation	95	No	Ground-dwelling invertebrates	Generic
	Fleay's barred frog (*Mixophyes fleayi*)	Wet forests	80	No	Insects, small frogs	Generic
	Southern barred frog (*Mixophyes iteratus*)	Leaf litter in rainforests and eucalypt forests	115	No	Insects, spiders and small frogs	Generic
	Northern Corroboree frog (*Pseudophryne pengilleyi*)	Beneath leaf litter, logs and dense ground cover	30	No	Small ants and other invertebrates	Blackberry (*Rubus fructicosus*)

a particular species may vary according to the degree of habitat specialisation. Habitat specialists may be more sensitive to habitat modification by exotic plants than generalist species with a broader niche range. While literature on this matter is depauperate in relation to reptiles and amphibians, insect herbivore assemblages on exotic plant hosts consist of generalist rather than specialist species (Brandle *et al*., 2008).

Home range size is an important factor relevant to the effect of changes in habitat structure on an individual reptile or amphibian. Species with smaller home ranges will have a greater proportion of their environment modified, be less able to respond to deleterious environmental changes by relocating or avoiding unsuitable areas and will be affected at a lower level of exotic plant coverage, than species with large home ranges. For species with smaller home ranges, a given area of exotic plant coverage may also affect a larger number of individuals than species with larger home ranges. Equally, advantageous changes to habitat structure (e.g. increasing availability of cover) are likely to exert their influence more strongly on species with a smaller home range as less coverage is needed to provide benefit to a greater number of individuals.

Body size and home range in lizards are positively correlated (Turner *et al*., 1969; Perry & Garland, 2002). In this respect, body size may in part, predict sensitivity to presence and area of exotic plants. However, the relationship between body size and home range is complicated by other influences such as diet, foraging mode, sexual dimorphism and phylogenetic differences (Rose, 1982; Christian & Waldschmidt, 1984; Perry & Garland, 2002) and a number of studies estimating home ranges have suffered from small sample sizes (Rose, 1982). Nevertheless, influence on home range size is not the only way in which body size may be important in influencing the responsiveness of reptiles and amphibians to exotic plant incursion. Body size can also influence the sensitivity of ectotherms to changes in thermal conditions of their environment.

Thermoregulation and maintenance of body temperature within appropriate ranges for various levels of activity is a key physiological task for many ectotherms. Considerable activity may therefore be devoted to thermoregulatory behaviour and selection of appropriate microclimates (Heatwole & Taylor, 1987). In many reptile and

amphibian species this includes 'shuttling' between sun and shade or warm and cold substrates or water in order to maintain body temperature within appropriate ranges (Heatwole & Taylor, 1987; Duellman & Trueb, 1994; Shine, 1998). Changes to insolation and shading as a result of altered vegetation structure will have an impact on the availability and suitability of basking sites, shaded areas and the tendency of substrates to absorb and maintain heat energy. For instance, thermal conditions and shading directly influence habitat preferences of the scincid lizards *Carlia vivax* and *Lygisaurus foliorum* in subtropical areas of northern Australia (Singh *et al*., 2002). Alteration of thermal conditions and shading by exotic plants is highly likely to influence the nature of reptile and amphibian assemblages. Smaller ectotherms exhibit more rapid rates of heating and cooling than larger animals (Heatwole & Taylor, 1987; Shine, 1998). Furthermore, smaller lizards shuttle between sun and shade more frequently than do larger lizards (Bowker, 1984; Heatwole & Taylor, 1987). There is strong evidence that smaller lizards may be more sensitive to modification of shade and basking sites brought about by exotic plants.

An emerging area of investigation is the extent to which different growth forms or functional groups of exotic plants differ in their impacts on ecological communities. Impacts are likely to be most severe where an exotic plant represents a growth form that is absent or is a minor component in the community subject to invasion (Grice, 2004). Investigation of thirteen invasive plant species in the Czech Republic revealed marked differences in their impact on species richness and evenness of invaded plant communities (Hejda *et al*., 2009). Severity of impact was highly specific to particular invaders and strongly influenced by the difference between the cover and height of the invader and native dominant species. By contrast, a review of the impacts of graminoid and woody invasive species showed few differences in their effects on most native plant functional groups (Mason *et al*., 2009).

In contrast to studies showing significant effects of exotic plants on animal assemblages, Sax (2002) found little difference in species richness and diversity of understorey plants, leaf-litter invertebrates, amphibians and birds between plantations of the exotic eucalypt (*Eucalyptus globulus*) and native woodland

dominated by coast live oak (*Quercus agrifolia*) and California bay tree (*Umbellularia californica*). Species composition did, however, vary between exotic and native vegetation. In that system understorey plants were apparently more important in determining diversity and composition of faunal assemblages than were trees, providing further evidence that the impact of exotic plants may vary with growth form and structural features.

I have noted the importance of home range size in influencing the responsiveness of reptile and amphibian species to exotic plant invasion. The corollary of this is that coverage, or stand size, of exotic plants will be an important factor determining their influence on reptiles and amphibians. Larger coverage or stand size may be required to exert impacts on species with larger home range. Thus, coverage will influence both the degree of effect exerted on an individual species and the number of species affected within an assemblage.

(*b*) *Predictions*

Considering the interaction between life-history traits of reptiles and amphibians and exotic plants, and mechanisms of impact, allows the formulation of specific predictions of the response of reptile and amphibian species and assemblages to changes in habitat structure caused by the incursion of exotic plants (see the top section of Fig. 2.1).

Prediction 1: there will be a positive correlation between habitat diversity and/or availability of cover, such that decreases in habitat diversity and cover will lead to declines in species richness and abundance of reptiles and amphibians. Increases in habitat diversity and cover will lead to increases in reptile and amphibian abundance and species richness.

Prediction 2: smaller-bodied species, and species with smaller home ranges, will display greater sensitivity and faster response to exotic plant invasion than larger-bodied species and species with larger home ranges. The latter require a greater area of coverage of exotic plants for effects to be discernible and would be expected to

show slower responses to exotic plants due to the time needed for exotic plants to spread and increase their area of coverage (see Fig. 2.1).

Prediction 3: habitat specialists will display stronger and more rapidly detectable responses to exotic plant invasion than generalist species.

Prediction 4: exotic plants exhibiting novel growth forms or structural features will exert stronger and more rapid influences on reptiles and amphibians via changes to habitat structure and quality, including leaf litter structure and availability of woody debris, than exotic plants that replicate existing growth forms and structural features.

Prediction 5: the degree of influence exerted on individual species and the number of species affected within an assemblage will increase with coverage of exotic plants.

(*c*) *Empirical evidence to support framework*

Avoidance of the introduced rubber vine (*Cryptostegia grandiflora*) occurred in Australian scincid lizards *Carlia munda* and *Carlia pectoralis* (Valentine *et al*., 2007). This provides supporting evidence for prediction 1, as avoidance of introduced plants may well lead to declines in species richness and abundance. Specifically, both species avoided rubber vine leaf litter when allowed to select between rubber vine and native leaf litter in semi-natural enclosures (Valentine *et al.*, 2007). The same investigation noted that rubber vine leaf litter was cooler at the surface than native leaf litter, supporting my hypothesis that alteration of habitat structure by exotic plants may have important impacts on thermal conditions. Similarly, there was a strong influence of exotic pine (*Pinus* spp.) on reptile assemblages in the tropics of northern Australia. Pine plantations were cooler and received less radiant energy than native forests. Reptile assemblages in these pine plantations comprised mostly closed-canopy rainforest species that prefer cooler, shadier habitats in contrast to surrounding native vegetation, which supported open woodland species (Mott *et al*., 2010). The long-term decline of the natterjack toad (*Epidalea calamita*) in heathland areas of Britain (Beebee, 1977) was related to overgrowth by pine (*Pinus* spp.), birch (*Betula* spp.), gorse (*Ulex* spp.) and bracken (*Pteridium* spp.) following land-use changes, reducing availability of basking sites for adult toads.

Alteration of habitat structure, including leaf litter structure and availability of woody debris influences reptile assemblages. Griffin *et al*. (1989) recorded reduced abundance of reptiles in parts of inland northern Australian where the exotic tamarisk (*Tamarix aphylla*) had replaced native river gum (*Eucalyptus camaldulensis*) vegetation. Tamarisk reduced the availability of potential cover for reptiles because there were fewer dead branches and logs on the ground. In addition, branches and logs that were present on the ground lacked the thick, persistent bark of eucalypt logs. Garden *et al*. (2007) reported that abundance of native reptiles was positively correlated with a moderate amount of exotic plant cover in urban forest fragments in Brisbane, Australia. Low weedy vegetation provided cover for reptile species and was more important than vegetation composition in determining terrestrial reptile assemblages. Mott *et al*. (2010) observed that burning under pine plantations in tropical northern Australia was associated with increased species richness and abundance of reptiles when compared with unburnt pine forests. Operative environmental temperatures and radiant energy were similar in burnt and unburnt pine. Avoidance of weedy leaf litter was responsible for lower species richness and abundance of reptiles in unburnt pine and removal of weedy litter by burning produced more favourable habitat conditions for reptiles. While these studies provide strong evidence for this prediction in relation to reptiles, the relative lack of studies examining the impacts of exotic plants on amphibian species and assemblages means that evidence relating to amphibians is lacking. This highlights the pressing need for further research to identify the influence of exotic plants on habitat structure for amphibians and their assemblages.

As a preliminary test of whether small body size (prediction 2) and an insectivorous diet (see Model 2, predictions 1 and 2) are linked to the listing of reptile species as threatened by exotic plants, I performed an analysis that modelled threat status of Australian reptile species (binary response variable) as a function of body size and diet (continuous and categorical explanatory variables, respectively) using a generalized linear model (binomial probability distribution with a logit link function) in SPSS v.17. Analysis of 757 species for which reliable data were available

(13 threatened, 744 non-threatened) found that neither body size (Wald $\chi^2 = 0.0001$, $P = 0.99$), diet (Wald $\chi^2 = 2.10$, $P = 0.35$), nor their interaction (Wald $\chi^2 = 1.99$, $P = 0.37$) was significantly related to threat listing. It is important to note that threatened species lists do not identify species (or individual populations) that may be affected by exotic plants but have not declined sufficiently to be classified as threatened. Nor do they identify species that may benefit from the presence of exotic plants. To address these limitations, further testing of prediction 2 is required. This should include a more comprehensive analysis of threatened species lists (i.e. at a global or multiple continent scale) and field investigations of variations in species composition between areas invaded by exotic plants and uninvaded, native vegetation. Such investigations would also allow prediction 3 to be tested.

A negative correlation was observed between per cent cover of introduced Sahara mustard (*Brassica tournefortii*) and abundance of fringe-toed lizards (*Uma inornata*) in active desert dune habitats in the Coachella Valley (Barrows & Allen, 2010). While this provides some support for prediction 4, further studies examining multiple exotic plant species of varying growth form, structural features and stand size are required to test this prediction, as well as prediction 5, in more critical detail. Further studies specifically examining amphibians and exotic plants should be viewed as a high priority as the current paucity of such studies limits the ability to assess these predictions in relation to amphibians.

2.2.2 Model 2: alteration of herbivory and predator-prey interactions

(*a*) *Theory*

Reptile and amphibian diets vary widely among species. Reptiles may be herbivorous, omnivorous or carnivorous, however, complete herbivory is not common (Heatwole & Taylor, 1987; Pough *et al*., 2004). Available information indicates that all adult amphibians are carnivores, however, larval diets may include plant matter, phytoplankton and aquatic invertebrates as well as amphibian eggs and larvae

(Duellman & Trueb, 1994). Dietary preferences may play an important role in determining the responsiveness of a species to exotic plant invasion.

Excluding native plant species and creating monocultural stands of exotic species represents a direct mechanism of impact on herbivores, by changing forage availability (Sax, 2002). Herbivores might well respond strongly and rapidly to the incursion of exotic plants, where this incursion either reduces availability of native plant food sources or introduces novel food. Changes to invertebrate assemblages brought about by exotic plant invasion may, in turn, exert impacts on vertebrates by altering the availability and composition of prey species for insectivores (Herrera & Dudley, 2003; Greenwood *et al*., 2004). Invertebrates are an important component of the diet of many reptile and amphibian species. For example, most lizards and frogs are invertebrate predators (Vitt & Pianka, 2007; Wells, 2007). Changes to invertebrate abundance and species richness, therefore, have the potential to exert major influences on herpetofauna - an influence likely to be exerted most strongly and rapidly in species for which invertebrates are a major component of the diet. Changes to abundance of invertebrate predators will subsequently exert impacts on species preying predominately on smaller reptiles and amphibians. Thus, indirect impacts on species consuming smaller reptiles and amphibians would be detectable later than direct impacts on insectivores.

Exotic plants may have differential effects on the availability of food for reptiles and amphibians as a function of time since introduction. For example, richness of herbivores and pest species of exotic species may increase with time since introduction (Strong *et al*., 1977; Frenzel *et al*., 2000; Brandle *et al*., 2008). Longer times since invasion provide increased opportunities for native species to adapt to exploiting new hosts (Carpenter & Cappuccino, 2005). Comparisons of ecological assemblages between exotic and native vegetation have also revealed a significant effect of plantation age (Sax, 2002). Specifically, species richness in older plantations compared with younger plantations more closely resembled native. In particular, species richness of mammals at several sites within Australian *Pinus radiata* plantations less than five years old was lower than in native forests; however, sites within older plantations had

species richness as high as sites within native forests (Friend, 1982). Similarly, bird diversity in seven-year-old plantations of exotic *Albizia falcataria* in Borneo was as high as native forests but lower in younger plantations (Mitra & Sheldon, 1993). Such increases in species richness and diversity with the age of a stand of exotic vegetation may be due to ecological succession and differences among species in the time required to colonise these habitats (Sax, 2002).

The effect of intraspecific niche partitioning in relation to diet is important. Such intraspecific niche partitioning may be related to ontogenic shifts in diet or sexual size dimorphism (Duellman & Trueb, 1994; Shine, 1998; Shine & Wall, 2007; Vitt & Pianka, 2007). Specifically, in a number of species, prey type changes with body size, as larger individuals can capture, subdue and consume larger prey, while foraging ability and strategy may also vary according to size (Shine & Wall, 2007). For example, juveniles of some ophidian species feed on small lizards or frogs while adults consume larger mammalian prey (Shine, 1998). Thus, dietary impacts of exotic plants vary within species according to age and gender.

Insect herbivore assemblages on exotic plants may be dominated by generalist species (Brandle *et al*., 2008), raising important questions about the role of dietary specialisation on the response of reptile and amphibian species and assemblages to exotic plants. Herbivorous lizards and tortoises often feed on a small number of plant species or particular parts of plants such as younger, less fibrous leaves (Pough *et al*., 2004). Replacement of these specialised food sources will have a direct and rapid impact on specialised herbivore species. Specialist insect predators would also be more vulnerable to reductions in species richness and abundance of insect herbivores, as only small changes in plant composition may be required to cause the reduction or loss of specific foods.

Home range and body size may also influence the extent to which an individual reptile or amphibian will be affected by changes to food availability due to incursion of exotic plants. Species with smaller home ranges cannot avoid areas with diminished forage, and, thus, less forage coverage may affect more individuals. Advantageous

changes to habitat for some reptile and amphibian species are likely to occur earlier in species with small home ranges. Here, less cover is needed to benefit more individuals.

Reptiles and amphibians are important prey items for a wide range of vertebrate predators as well as predatory arthropods (Duellman & Trueb, 1994; Shine, 1998; Wells, 2007). Changes to habitat structure may increase or decrease the vulnerability of reptiles and amphibians to predation by altering the availability of cover and refuge sites. Furthermore, small reptiles and amphibians are more likely to be easy prey than larger animals for predators. Thus, the effects of structural changes to habitat by exotic plants will interact with animal body size. In addition, novel growth forms and structural features of exotic plants are likely to exert the strongest impact on the vulnerability of reptiles and amphibians to predation as they will produce the greatest change in habitat structure.

There is a growing body of evidence indicating that taxonomically distinct exotic plants (compared with native vegetation) will have stronger influences on the abundance and richness of herbivorous invertebrates. In particular, taxonomically distinct or isolated exotic plant species are likely to have reduced herbivore abundance and richness (Frenzel *et al*., 2000; Agrawal & Kotanen, 2003; Brandle *et al*., 2008).

(*b*) *Predictions*

From these theoretical considerations, I derive a number of predictions regarding the response of reptile and amphibian species and assemblages to altered herbivory and predator/prey interactions by exotic plants (see central section of Fig. 2.1).

Prediction 1: responses to changes in herbivory and predator-prey interactions will be stronger and detectable earlier in small-bodied and small-home-range species. Species with large body size and large home range will be less responsive to invasion and be affected more slowly.

Prediction 2: response to alteration of the availability of forage will be strongest and detectable earliest in herbivorous and insectivorous species, especially if coupled with even finer dietary specialisation. Dietary generalist species and species that prey on vertebrates will respond more slowly.

Prediction 3: dietary variation due to ontogenic shifts and/or sexual size dimorphism will have differential impacts within a population. While long-term viability of a population may be compromised, this may not be readily detected within the limitations of short-term fauna survey and monitoring programs.

Prediction 4: exotic plants with novel growth forms and structural features will exert stronger and more rapidly detectable influences on herbivory and predator/prey relationships than exotic plants that are similar to native plants.

Prediction 5: taxonomically distinct exotic plants, compared with native vegetation, will exert stronger influences on the availability of forage for insectivores.

Prediction 6: larger coverage of exotic plants will equate to stronger influences on feeding ecology of reptiles and amphibians and more species will be affected.

Prediction 7: species richness and/or abundance of reptiles and amphibians may increase over time if the abundance and diversity of invertebrates increases. This requires the existence of remnant reptile or amphibian populations in the affected area or colonisation from nearby populations. The effect would be observed in insectivores before any detectable response in species preying mainly upon reptiles and amphibians.

(*c*) *Empirical evidence to support framework*

Evidence to support predictions 1 and 2 is provided by the avoidance of introduced rubber vine (*Cryptostegia grandiflora*) by the scincid lizards *Carlia munda* and *Carlia pectoralis* in northern Australia (Valentine *et al*., 2007). These are small-bodied (snout-vent length 44-52 mm) insectivorous lizards occurring in forest litter (Wilson & Swan, 2010). Rubber vine litter contained significantly different arthropod taxa than native leaf litter, with fewer preferred prey items of *C. munda* and *C. pectoralis*. In addition, rubber vine leaves were a different shape than the elongate native leaf litter, providing less suitable cover with potentially decreased camouflage. Reduced reptile richness was associated with declines in arthropod abundance in weed-infested habitat in northern Australia (Griffin *et al*., 1989).

Incursion of Japanese knotweed (*Fallopia japonica*) into foraging areas adjacent to wetlands has reduced the foraging efficiency of frogs (*Rana clamitans*) in New York (Maerz *et al*., 2005). Frogs confined to areas invaded by Japanese knotweed for 38 h showed significant declines in mass compared to frogs confined to uninvaded areas. Invasion by Japanese knotweed was associated with significant changes in vegetation structure and composition and invasion degraded terrestrial habitat quality for frogs by reducing arthropod abundance. Analysis of body size and diet of Australian reptiles (see Section 2.2.1) did not identify any clear-cut link between listing as threatened by exotic plants and diet, or body size and diet combined. More comprehensive analysis of the life-history traits of species threatened by exotic plants and field investigations are required to test these predictions thoroughly.

The relatively small number of investigations of exotic plant impacts on reptiles and amphibians provide limited evidence for predictions 3–7. Testing of predictions 3 and 4 will require detailed investigations of variations in species composition, population dynamics and diets of reptile and amphibian communities between areas invaded by exotic plants and uninvaded, native vegetation. Such investigations would also test predictions 1 and 2 further. Studies examining multiple exotic plant species of varying taxonomic distinctiveness, growth form, structural features and stand ages are required to test predictions 5–7.

2.2.3 Model 3: modification of reproductive success

(*a*) *Theory*

Exotic plant invasion may restrict access to oviposition sites for reptiles and amphibians and alter conditions for the incubation and growth of embryos and larval offspring. The extent to which vegetation changes from exotic plants affect reproduction of reptiles and amphibians will be influenced by the nature of the exotic species and the reproductive biology of the reptile and amphibian species. In particular, viviparous species should be less susceptible to this effect, as gravid females do not require access to oviposition sites and can exert greater control over incubation temperatures by thermoregulating (Heatwole & Taylor, 1987). Incubation

temperatures can influence the growth and development of reptilian embryos, including sex determination. Growth and differentiation of amphibian larvae are also temperature dependent (Wells, 2007).

Oviparous and viviparous modes of reproduction represent opposite ends of a continuum, with variations among species in the developmental stages of embryos at the time of oviposition (Heatwole & Taylor, 1987; Shine, 1998). Also, both modes of reproduction may be present in different parts of the ranges of some squamate species (Shine, 1998). Vulnerability to inhibition of embryonic development and biasing of sex ratios may therefore vary among species (or populations) depending on the degree of embryonic development at oviposition. Thus, species which exhibit oviposition immediately following ovulation such as chelonians, crocodilians and some squamates (Heatwole & Taylor 1987) would be most vulnerable and viviparous species least vulnerable.

A higher proportion of viviparous species occur in colder habitats (Shine, 1985*a*, *b*, 1998) and some cold-climate areas contain only viviparous species (Shine, 1998). Viviparity in amphibians is also one of several reproductive strategies that have allowed them to occupy montane environments (Duellman & Trueb, 1994). Thus, interference with oviposition by exotic plants will affect fewer species and exert less influence on the structure of reptile and amphibian assemblages in colder climates.

Parental transport of eggs, tadpoles and froglets occurs in a number of anuran species (Duellman & Trueb, 1994; Wells, 2007). Parental transport may confer similar advantages to viviparity in reducing vulnerability of frogs to altered thermal conditions. Adults can avoid unfavourable conditions and select sites that are independent of oviposition locations. Species with parental transport would be less likely to show impacts from exotic plants on reproductive success compared with species without parental transport.

Temperature sensitivity to sex determination will play a role in the sensitivity of reptile and amphibian species to changes in thermal conditions for eggs and larvae linked to exotic plant invasion. As with other vertebrates, sex-determination mechanisms in reptiles and amphibians may be classified as genotypic sex

determination (GSD) or environmental sex determination (ESD) (Bull, 1983; Hayes, 1998; Shine *et al.*, 2002; Quinn *et al*., 2007). ESD, where temperature at the time of embryonic development is the determining environmental factor, may also be classified as temperature-dependent sex determination (TSD) (Quinn *et al*., 2007). Generally, amphibians have GSD (Wallace *et al*.,1999), but TSD has been observed in many reptile species, particularly those lacking heteromorphic sex chromosomes such as crocodilians, chelonians and some squamates (Heatwole & Taylor, 1987). Species exhibiting TSD will, therefore, be vulnerable to biasing of sex ratios due to altered incubation conditions.

Exotic plant invasion is more likely to affect species with a narrow range of oviposition sites than those capable of utilising a broader range of sites. Some anuran species are highly plastic in their choice of oviposition sites, while others have more specific requirements (Wells, 2007). This effect will be compounded for species or populations that employ communal nesting and that reuse nesting sites each breeding season. For instance, communal nesting in the Australian elapid *Demansia psammophis* can involve in excess of 500 eggs (the product of almost 100 females) at a single site, along with many egg shells from previous years (Shine, 1998). The loss or reduced suitability of such communal nesting sites could have a significant impact on local populations of these species.

The life spans and generation times of reptiles and amphibians will interact with exotic plant invasion. Loss of incubation sites for short-lived, early maturing species, where failure of a single breeding season may cause a severe reduction in the population (Heatwole & Taylor, 1987) will produce stronger and more rapidly detectable population declines than longer lived and later maturing species, in which adults may persist despite reduced reproductive success. In addition, changes to the accessibility, suitability and number of oviposition sites due to increased cover and overshadowing by exotic plants will be more noticeable in exotic plants with novel growth forms or structural features.

(*b*) *Predictions*

I provide predictions of the impact of exotic plants on reptile and amphibian reproduction (see bottom section of Fig. 2.1).

Prediction 1: incursion of exotic plants into native vegetation will influence the abundance and richness of reptiles and amphibians by restricting access to oviposition sites and altering incubation and growth of larval offspring.

Prediction 2: these impacts will be more substantial and rapid in species whose reproductive strategies include oviparity, lack of parental transport of eggs, larval young and/or froglets, strong influence of temperature in sex determination, short life span, short generation times and a narrow range of oviposition sites. Traits such as viviparity, parental transport, longer life span and generation times, genotypic sex determination and plasticity in oviposition sites will correspond to weaker and less rapidly detectable impacts.

Prediction 3: exotic plants will have less impact on reptile and amphibian reproduction in cold-climate areas where a higher proportion of viviparous species are likely to occur.

Prediction 4: exotic plants with novel growth form or structural features will exert stronger and more rapid effects on reptiles and amphibians by changing thermal conditions, compared with exotic plants that are similar to existing growth forms and structural features.

Prediction 5: increasing coverage of exotic plants will be positively correlated with increasing impacts on the reproduction of individual species and the number of species affected within an assemblage.

(*c*) *Empirical evidence to support framework*

There is strong support from the literature for prediction 1. Invasion of riparian areas by an exotic plant *Chromoleana odorata* prompted female Nile crocodiles (*Crocodylus niloticus*) in South Africa to abandon digging egg chambers when fibrous root mats were encountered (Leslie & Spotila, 2001). Further, soil temperatures in sites shaded by *Chromoleana odorata* were cooler than those of unshaded sites, potentially

creating biased sex ratios of offspring or completely preventing embryonic development. Interference with nesting of the American crocodile (*Crocodylus acutus*) and sea turtles also occurs in parts of south-eastern Florida subject to incursion of the exotic *Casuarina equisetifolia* (Austin, 1978).

A similar impact of exotic vegetation on nesting sites has been identified for the endangered Mary River turtle *(Elusor macrus*) in Queensland, Australia with exotic plants such as lantana (*Lantana camara*), para grass (*Urochloa mutica*) and various species of thistle (family Asteraceae) blocking access to nesting sites (Tucker, 1999; Department of Environment, Water, Heritage and the Arts, 2009). Destruction of eggs by penetration of couch grass roots (*Cynodon* sp.) has also been identified at nesting sites (van Kampen *et al*., 2003; Department of Environment, Water, Heritage and the Arts, 2009).

Decline of the natterjack toad (*Epidalea calamita*) in Britain has been linked to vegetation change causing reduced suitability of breeding ponds (Beebee, 1977). Overshadowing and cooling from vegetation change contributed to the decline. Detailed investigations of the effect of shading of breeding ponds by exotic plants on the growth and maturation of amphibian eggs and larvae are also required to test this prediction further in relation to amphibians. The studies described above also provide examples of impacts on oviparous species (prediction 2), however, further investigations are required to test this prediction. Specifically, detailed comparisons of assemblages between invaded and uninvaded areas are required to examine whether there are any consistent differences in the reproductive traits of species present. Testing of prediction 3 will require investigation across a wide range of climatic regimes to determine whether impacts are exerted differentially between warm- and cold-climate areas. Studies examining multiple exotic plant species of varying growth form, structural features and stand size are required to test predictions 4 and 5.

2.3 Management implications and future research opportunities

Control and removal of exotic plant species are important aspects of many conservation programs. It is important, therefore, that such efforts be informed by the best available scientific knowledge of the impacts of exotic plants and the efficacy of removal strategies. The effects of growth form and structural features, stand age and spatial scale of exotic vegetation on ecological assemblages have important implications for conservation efforts, in particular for determining priorities for exotic plant removal and control programs. In the absence of detailed knowledge of these effects it is difficult to determine whether efforts and funding should be focused on removing older, established and larger stands of exotic vegetation, or preventing new stands from establishing and quickly removing exotic vegetation before severe impacts occur. Indeed, removal may have more dire consequences than leaving exotic species where they are. It is also difficult to predict which exotic plant species are most likely to produce undesirable effects and should be prioritised for management and control efforts. The framework presented here provides testable predictions of the impacts of exotic plants on reptiles and amphibians and the exotic plant traits most likely to produce these impacts.

Exotic species in both terrestrial and marine environments rapidly establish interactions with other species, raising questions as to whether it is possible to restore pre-invasion biota and ecology (Vermeij, 1996). Furthermore, care must be exercised in choosing control methods to avoid causing further deleterious impacts as certain methods may affect the ecology of the invaded community (Sakai *et al*., 2001). For example, control of the exotic vine *Clematis vitalba* in the North Island of New Zealand using a combination of mechanical removal, herbicides and sheep grazing can be as damaging to a site as the exotic vegetation itself (Ogle *et al*., 2000). Use of chemical sprays for weed control has been listed as a threat to a number of amphibian species including green and golden bell frogs (*Litoria aurea*) and the spotted tree frog (*Litoria spenceri*) (Department of Environment and Climate Change, 2009; Department of Environment, Water, Heritage and the Arts, 2009). Exotic plant removal without a revegetation plan may also result in soil disturbance or re-invasion by the same or

other exotic species (D'Antonio & Meyerson, 2002). This has clear implications for exotic plant removal and control strategies such as bush regeneration. It is, therefore, important to investigate further the effects of exotic plant removal on ecological systems.

There has been little attention given to the effects of management, control and removal of exotic plant species on reptiles and amphibians, however, removal of *Chromoleana odorata* from riparian areas increases the use of potential nesting sites by the Nile crocodile (*Crocodylus niloticus*) (Leslie & Spotila, 2001). There is a need for more detailed investigation of these factors. Specifically, studies involving multiple exotic plant species of varying growth forms, stand age and size as well as examination of the efficacy of management and control efforts would make valuable contributions to the understanding of the effect of exotic plants on reptiles and amphibians and the conservation of biodiversity.

2.4. Conclusions

(1) There are three mechanisms by which exotic plants can influence reptile and amphibian species and assemblages. These are changes to: (1) habitat structure; (2) herbivory and predator-prey interactions; and (3) reproductive success.
(2) Interactions between exotic plant and reptile and amphibian traits will determine the extent to which each of these mechanisms operate and the impacts on herpetofauna.
(3) There is limited evidence in the literature to support predictions that small-bodied, insectivorous and oviparous reptiles and amphibians will display the strongest response to invasion of exotic plants into native vegetation, however, further investigations are needed to test these predictions thoroughly.
(4) Evidence for model predictions is stronger for reptiles than for amphibians, in part due to the limited number of studies considering the effects of exotic plants on amphibians. There is an urgent need for quantitative research to test predictions in relation to amphibians and to increase knowledge of the impacts of exotic plants on amphibian species and assemblages.

(5) Further investigation is required to determine the importance of habitat and dietary specialisation and sex-determination mechanisms in reptiles and amphibians, and the influences of exotic plant growth form, stand age, coverage as well as taxonomic distinctiveness from native vegetation.

Chapter 3: How do native reptile assemblages respond to invasion by exotic plant species of differing growth form?

3.1 Introduction

The framework presented in Chapter 2 provides a number of testable predictions linking the traits of exotic plants to their impacts on reptiles and amphibians. At the same time, it captures the role of reptile and amphibian life-history traits in determining faunal sensitivity to the impacts of exotic plants. In this chapter, I present the results of field investigations that tested key predictions of the framework.

Reptile and amphibian assemblages are strongly influenced by vegetation structure and heterogeneity (Pianka, 1967; Heatwole & Taylor, 1987; Duellman & Trueb, 1994). Exotic plant invasion can substantially change vegetation structure, altering the characteristics and availability of habitat for reptiles and amphibians. The extent of vegetation change is related to the growth form of the invading species (Grice, 2004). Exotic plant species that are similar in growth form to native species in the invaded vegetation will modify habitats much less than exotic plant species that are remarkably different in growth form. For instance, the invasive shrub *Mimosa pigra* substantially alters floodplains in northern Australia that are normally dominated by herbaceous plants (Lonsdale, 1992; Grice 2004), while some exotic grasses such as Cocksfoot (*Dactylis glomerata*) invade grassland and bushland but are similar to the native ground flora they replace (Muyt, 2001).

Sensitivity of reptiles and amphibians to habitat changes brought about by exotic plant invasion will in turn be influenced by their own animal life-history traits. A key trait likely to influence sensitivity to alteration of vegetation structure is body size (see Chapter 2). Smaller-bodied reptiles generally have smaller home ranges (Turner, *et al.*, 1969; Perry & Garland, 2002). As a result, smaller-bodied species will have more of their habitat modified following exotic plant invasion and be less able to avoid unsuitable habitat than larger reptiles. In addition, smaller-bodied ectotherms exhibit faster rates of heating and cooling than larger-bodied species (Heatwole & Taylor,

1987; Shine, 1998) making them more sensitive to any changes in availability of light and shade as a result of habitat change by exotic plant invasion.

These considerations lead to two predictions derived from my framework that I test in this chapter:

1. Exotic plant species that differ substantially in growth form to native plants in the invaded vegetation will have a stronger and more rapid impact on reptiles and amphibians than exotic plants that are similar to existing plant growth forms;
2. Smaller-bodied reptile and amphibian species will be more sensitive to vegetation change brought about by exotic plant invasion compared with larger-bodied species.

I examined the ecological responses of reptile and amphibian assemblages to invasion by two exotic plant species, Lantana (*Lantana camara*) and Bitou Bush (*Chrysanthemoides monilifera* ssp. *rotundata*), both of which are Weeds of National Significance (WONS) and highly successful invaders of native vegetation in Australia (Australian Weeds Committee, 2010). In the study sites selected for this chapter, Lantana differed substantially to the dominant native growth form. In contrast, Bitou Bush provided a growth form replacement similar to native plants in the invaded vegetation (specific details of these habitat effects are presented in Chapter 5).

3.2 Methods

Lantana has invaded more than five million hectares of the Australian landscape and its invasive spread has been identified as a key threatening process causing biodiversity decline (NSW Scientific Committee, 2006). Invasion by Bitou Bush has also been identified as a key threatening process causing biodiversity decline due to its success as an invasive species and its impact on native flora and fauna (NSW Scientific Committee, 1999). Bitou Bush has invaded over 80% of the NSW coastline and is a serious threat to coastal areas in Victoria and Queensland (Australian Weeds

Committee, 2010). In NSW, Bitou Bush threatens more than 150 native plant species and 26 ecological communities (Australian Weeds Committee, 2010).

Investigation of Lantana impacts on reptiles and amphibians (hereafter the 'Lantana study') was conducted in dry sclerophyll forest vegetation. Lantana differs substantially to the dominant native vegetation in dry sclerophyll forest and alters habitat structure by replacing an open, sunlit understory with a dense, heavily shaded thicket (Fig. 3.1). Investigation of Bitou Bush impacts on reptiles and amphibians (hereafter the 'Bitou study') was conducted in coastal heathland areas. In these areas Bitou Bush is similar in growth form to the native vegetation it replaces. Habitat structure is similar in invaded and uninvaded areas with areas of low, dense native shrubs converted to areas of low, dense Bitou Bush (Fig. 3.2).

3.2.1 Site descriptions and experimental design

For both studies a multi-site comparison approach was used. This approach allows detailed assessment of exotic plant impacts over a relatively short time frame (Adair & Groves, 1998). Invaded and uninvaded sites were located within the same geographic regions with similar physical environmental conditions and proximity to disturbance.

3.2.1.1 Lantana study

A total of ten sites (five invaded and five uninvaded) were selected in national parks and public reserves in the Newcastle/Lake Macquarie area of NSW (Fig. 3.3). The area has a warm, temperate climate. Average annual rainfall is 1134.3 mm with highest rainfall in the period from February to June. Annual average maximum and minimum temperatures are 21.8^{o}C and 14.2^{o}C respectively. Warmest temperatures are recorded in summer with average daily temperatures of 19.2–25.5^{o}C in January. Coolest temperatures are recorded in winter with average daily temperatures of 8.4–16.7^{o}C in July (BOM, 2012). All sites were located near the coast at elevations between 5 and 111 m. Geographic location and elevation data for all sites are provided in Table 3.1.

(a) (b)

Fig. 3.1. Dry sclerophyll forest and invasion of *Lantana camara*. Uninvaded vegetation (a), invaded vegetation (b).

(a) (b)

Fig. 3.2. Coastal heathland and invasion of *Chrysanthemoides monilifera* ssp. *rotundata*. Uninvaded vegetation (a), invaded vegetation (b).

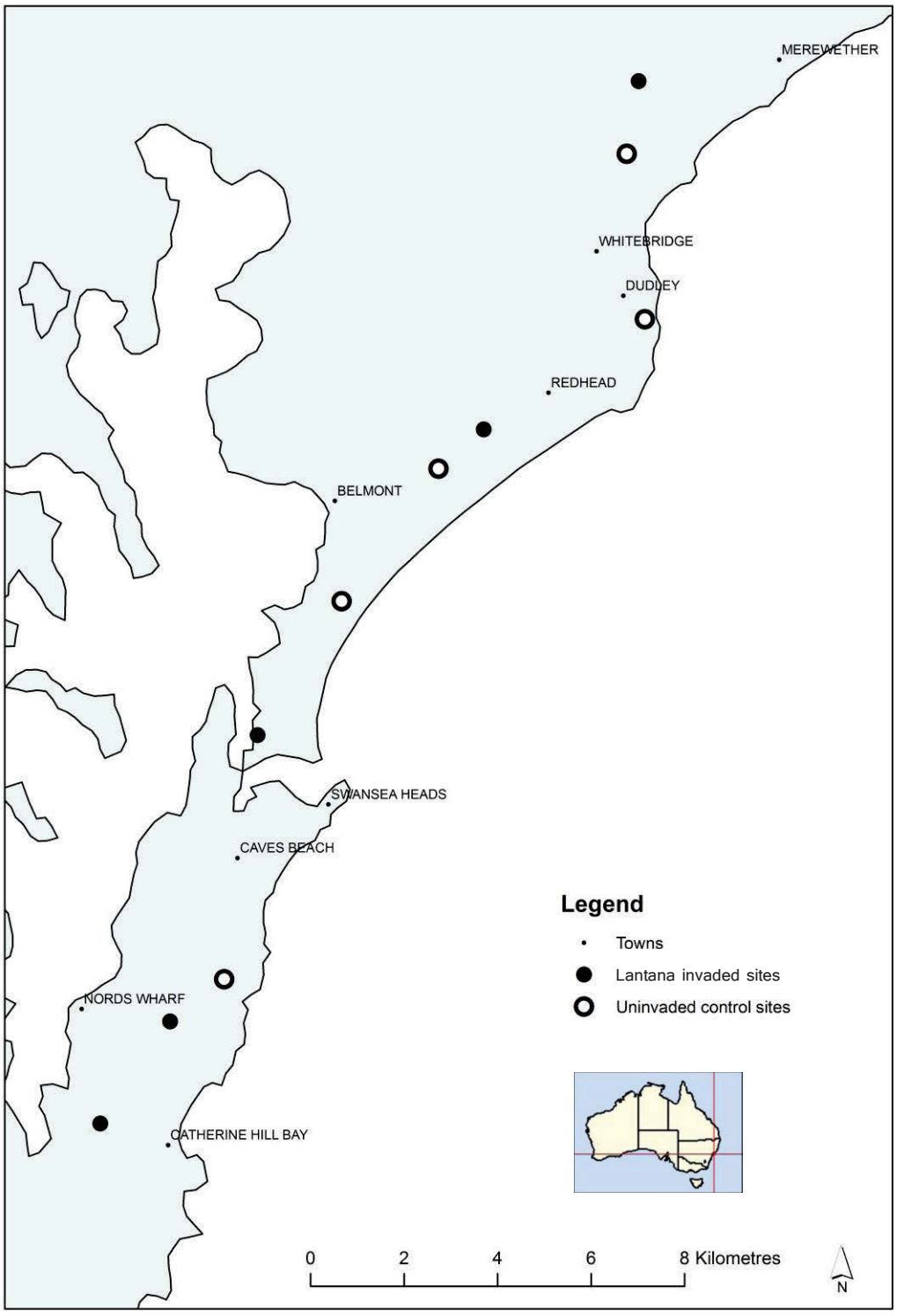

Fig. 3.3. Location of Lantana study sites in the Newcastle/Lake Macquarie area of NSW.

Table 3.1. Geographic location and elevation data for Lantana study sites. NP = National Park, SP = State Park, NR = Nature Reserve, SCA = State Conservation Area. All plot sizes = 50 m x 50 m.

Site	Latitude	Longitude	Elevation (m)
Control (no Lantana)			
LC1 Catherine Hill Bay, Wallarah NP	S33°7'33.9"	E151°38'18.5"	16
LC2 Belmont	S33°3'8.9"	E151°39'41.3"	5
LC3 Belmont Wetlands SP	S33°1'34.2"	E151°39'41.3"	13
LC4 Awabakal NR	S32°59'44.4"	E151°43'40.1"	106
LC5 Glenrock SCA	S32°57'50.5"	E151°43'19"	99
Invaded (Lantana)			
LI1 Nords Wharf, Wallarah NP	S33°9'17.5"	E151°36'41.8"	73
LI2 Catherine Hill Bay, Wallarah NP	S33°8'4.9"	E151°39'35.5"	29
LI3 Little Pelican Reserve	S33°4'44.1"	E151°38'37"	12
LI4 Belmont Wetland SP	S33°1'5.6"	E151°41'31.7"	6
LI5 Glenrock SCA	S32°57'0.1"	E151°43'26.1"	111

3.2.1.2 Bitou study

A total of ten sites (five invaded and five uninvaded) were selected in national parks and public reserves in the Botany Bay and Kurnell Peninsula area of Sydney, NSW (Fig. 3.4.) The area has a warm, temperate climate. Average annual rainfall is 1084.2 mm with highest rainfall in the period from February to June. Annual average maximum and minimum temperatures are 22.2°C and 13.4°C respectively. Warmest temperatures are recorded in summer with average daily temperatures of 18.8–26.5°C in January. Coolest temperatures are recorded in winter with average daily temperatures of 7.1–17.0°C in July (BOM, 2012). All sites were located near the coast at elevations between 7 and 42 m. Geographic location and elevation data for all sites are provided in Table 3.2.

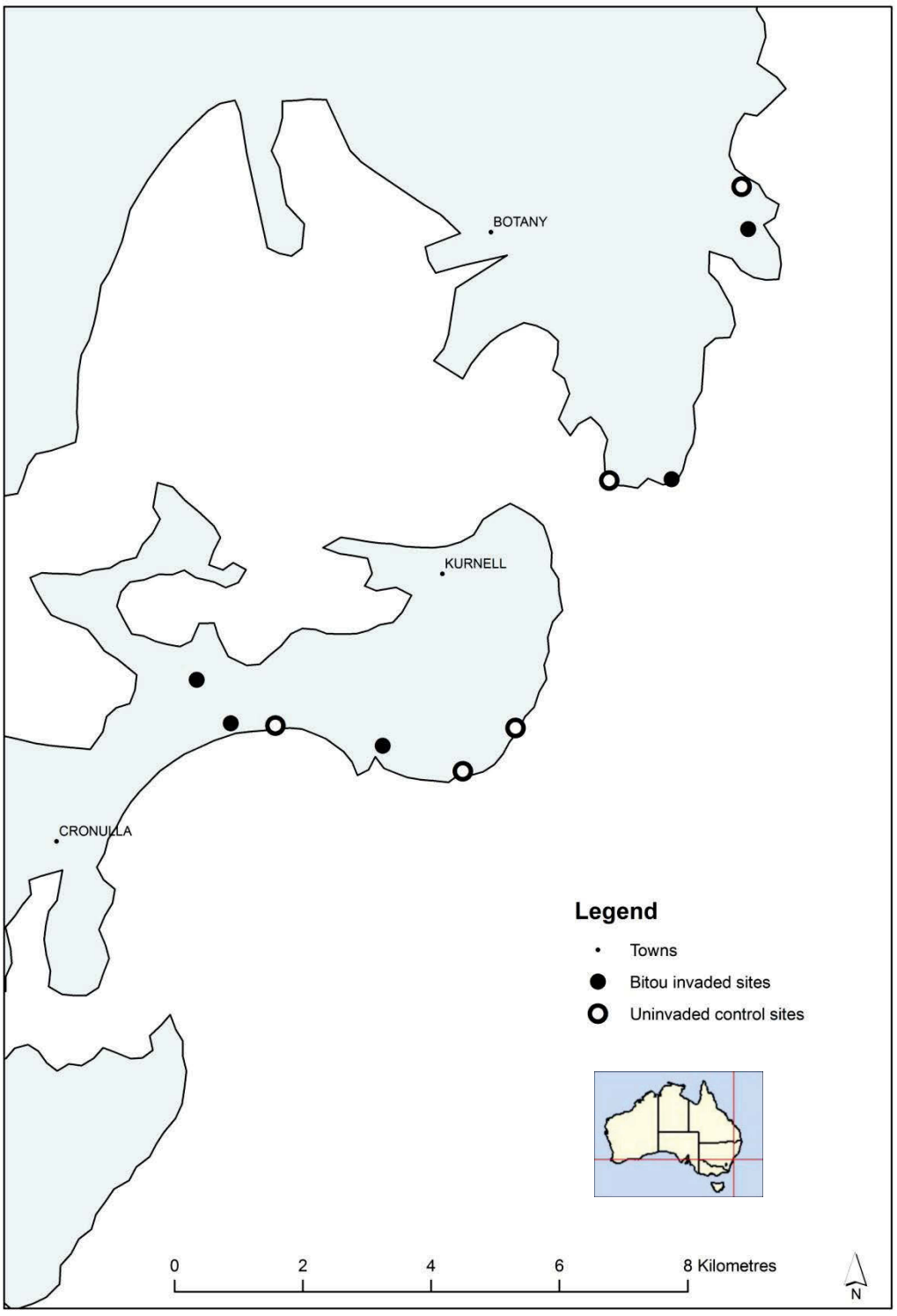

Fig. 3.4. Location of Bitou study sites in the Botany Bay and Kurnell Peninsula area of NSW.

Table 3.2. Geographic location and elevation data for Bitou study sites. NP = National Park. [1] = large plot (50 m x 50 m), [2] = small plot (50 m x 20 m), see 'Study sites' in the Methods for details about plot sizes.

Site	Latitude	Longitude	Elevation (m)
Control (no Bitou)			
BC1 Kurnell, Botany Bay NP 1[1]	S34°2'21.7"	E151°12'58"	24
BC2 Kurnell, Botany Bay NP 2[2]	S34°1'58.7"	E151°13'28.8"	42
BC3 Greenhills Reserve, Cronulla[2]	S34°2'10.6"	E151°11'3.1"	7
BC4 La Perouse, Botany Bay NP[1]	S33°57'20.8"	E151°15'32.2"	39
BC5 Malabar Headland control[1]	S33°59'51.8"	E151°14'19.4"	18
Invaded (Bitou)			
BI1 Kurnell, Botany Bay NP [2]	S34°2'10.6"	E151°12'8.6"	14
BI2 Greenhills Reserve, Cronulla[1]	S34°1'41.1	E151°10'14.3"	25
BI3 Charlotte Breen Reserve Kurnell[2]	S34°2'2.3"	E151°10'35.9"	8
BI4 La Perouse, Botany Bay NP[1]	S33°57'42.1"	E151°15'37.3"	32
BI5 Malabar Headland[1]	S33°59'50"	E151°14'57.2"	14

3.2.1.3 Study sites

An important consideration in multi-site comparison studies is the need to ensure that uninvaded sites are comparable to invaded sites (Adair & Groves, 1998). In this regard, I selected invaded and uninvaded sites that were homogeneous with the exception of considerable exotic plant invasion at the invaded sites. All study sites were located in vegetation adjacent to well-formed tracks or roads as Lantana and Bitou Bush primarily invade areas of disturbance. Sites were selected with no evidence of recent or ongoing weed control or recent fire as these could act as confounding factors influencing reptile assemblages. The minimum distance between any two sites was 1 km. Thick patches of Lantana and Bitou Bush comprised 40% cover on average at invaded sites and formed a mosaic with native vegetation in the Lantana study and the Bitou study respectively. In the Lantana study, the native vegetation at all sites was characterised

by trees such as Angophoras (*Angophora* spp.), and Eucalypts (*Eucalyptus* spp.) and understory shrubs such as Tea Trees (*Leptospermum* spp.), Wattles (*Acacia* spp.) and Grevilleas (*Grevillea* spp.). In the Bitou study, the native vegetation at all sites was characterised by low dense shrubs, such as Coast Wattle (*Acacia longifolia* var. *sophorae*), and Banksias (*Banksia* spp.).

In the Lantana study there were five large sites (50 m x 50 m; Fig. 3.5) which were located in invaded vegetation and five of the same size in uninvaded native vegetation. In the Bitou study, three large sites and two small sites (50 m x 20 m; Fig. 3.6) were used for invaded vegetation, with a matching number and type of sites in uninvaded vegetation. The two small sites were selected in place of large sites based on the limited availability of large sites which was determined after an exhaustive survey of the study area. The two small sites could not be extended in width to 50 m as marked changes in the slope of the sites precluded slope remaining constant across the sites.

3.2.2 Reptile and amphibian sampling

Reptile and amphibian surveys were conducted at each site in March/April 2010 (autumn), November 2010 (spring) and February 2011 (summer). Permanent 4 m wide x 50 m long search transects were established within each study site, running parallel to the vegetation edge. The first transect was located 2.5 m from the edge and further transects were positioned at 15 m intervals from each other and away from the vegetation edge, parallel with the first transect. Four transects (a total search area of 800 m^2) and two transects (total search area 400 m^2) were used in large (Fig. 3.5) and small (Fig. 3.6) plots respectively. Data for each transect within a site were combined to give abundance and species richness totals for each site (standardised per 100 m^2 of transect). This arrangement was used to ensure consistency of sampling effort in the disturbed edges and to ensure that, in each survey, stands were thoroughly searched without re-sampling any previously searched parts of a site.

Reptiles and amphibians were sampled once per season using time constrained, diurnal active searches. Order of site visits during each survey period was

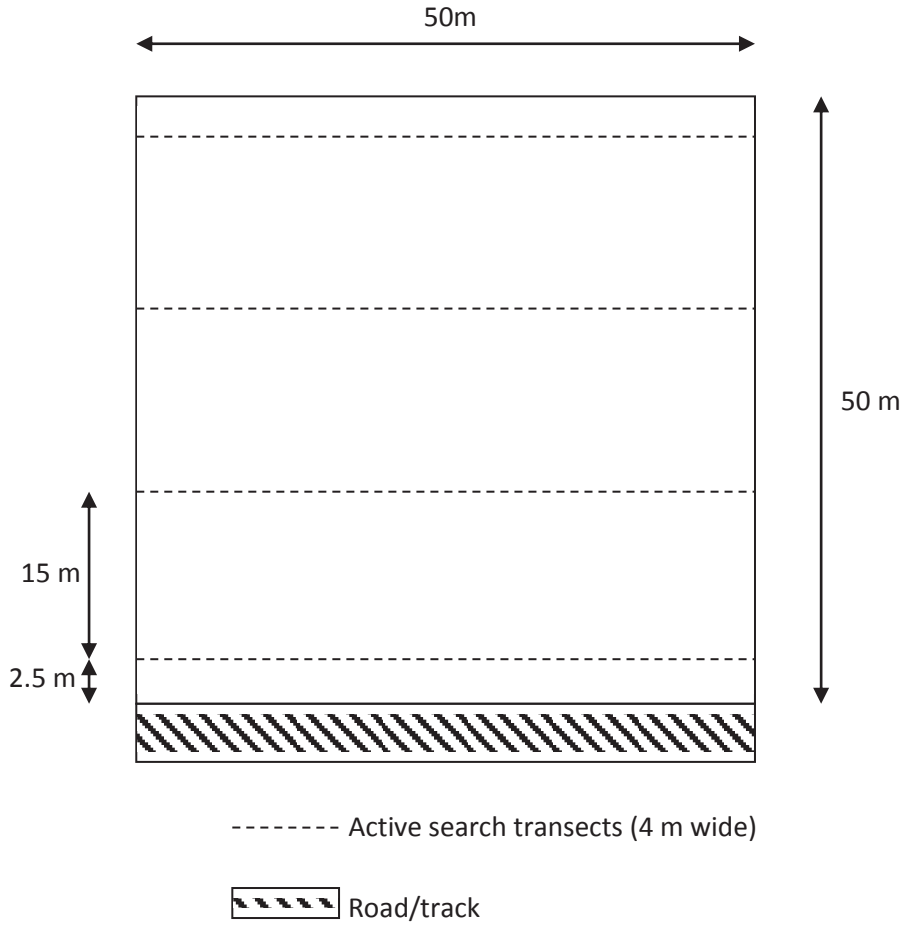

Fig. 3.5. Schematic representation of large (50 m x 50 m) study plots

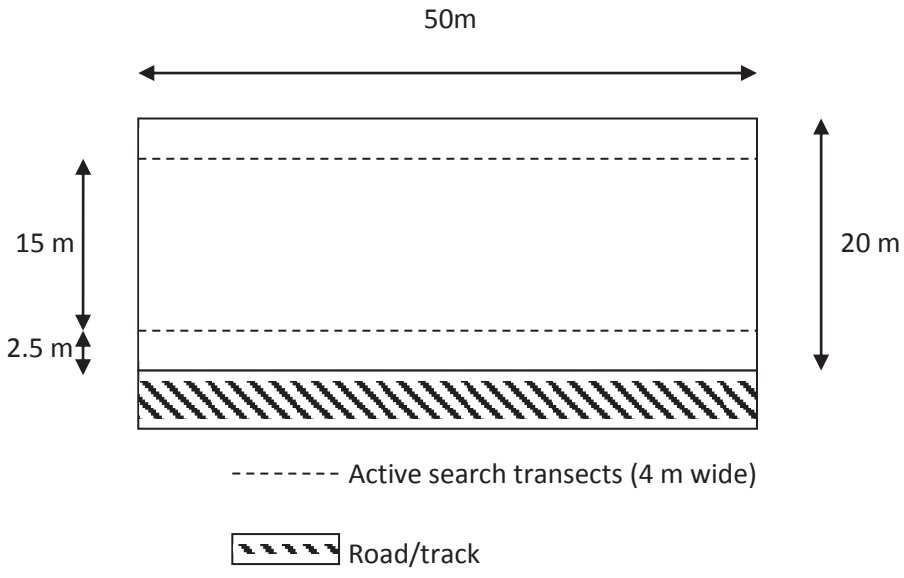

Fig. 3.6. Schematic representation of small (50 m x 20 m) study plots

randomised. All searches were conducted in warm, sunny conditions with ambient temperatures in excess of 20^{o}C and between the hours of 0900 and 1100 Eastern Standard Time (EST) or 1500 and 1700 EST. Searches were constrained to 15 minutes per transect (total 60 minutes per large site and 30 minutes per small site) and consisted of haphazardly turning rocks and logs, lifting loose bark and raking leaf litter along each transect. Duration of time constrained searches was based on a pilot assessment of the time required to efficiently search a transect. Surface active reptiles sighted within 2 m of either side of the centre line of each transect were also recorded. Pitfall traps and drift-fences were not used as additional sampling methods. Shallow, rocky soils at a number of sites precluded the use traps deep enough to prevent escape of trapped animals. Installing drift fences would have required removal Lantana and Bitou Bush, confounding the effects of invasion. All reptiles and amphibians were readily identified to species level, including the closely-related and similar-sized *Lampropholis delicata* and *L. guichenoti*, which were distinguished by the heavier build and dark vertebral stripe of *L.guichenoti* (Griffiths, 2006). Reptile taxonomy follows Wilson and Swan (2010); amphibian taxonomy follows Tyler and Knight (2011).

In the Lantana study one control site (LC2 Belmont) and one invaded site (LI3 Little Pelican Reserve) could not be sampled in spring 2010. Access to these sites during the spring survey period was prevented by localised flooding.

In the Bitou study, two invaded sites (BI1 Kurnell and BI4 La Perouse) were subjected to herbicide treatment of Bitou Bush by the NSW National Parks and Wildlife Service soon after the completion of the autumn 2010 survey. The unexpected spraying of herbicide at these sites resulted in near to 100% mortality of Bitou Bush at the two sprayed sites and prevented their use in comparisons between invaded and uninvaded vegetation in the spring 2010 and summer 2011 surveys for the purposes of the predictions of this chapter. Surveys at the two sprayed sites were, however, carried out in spring 2010 and summer 2011 as the spraying of Bitou Bush provided an unplanned opportunity to conduct a multiple before-after reference control-impact (M-BARCI) study to examine the response of reptile communities to control of Bitou Bush with herbicide (see Chapter 4).

3.2.3 Statistical analyses

Reptile abundance and species richness were analysed using separate general linear models (GLMs) in SPSS v.20. 'Condition' (invaded or uninvaded) and 'Time' (autumn 2010, spring 2010, summer 2011) were fixed factors and an interaction term for Condition x Time was included in the model. Data for abundance and species richness were ln(x + 1) transformed to improve normality and homogeneity of variances. Graphs depict untransformed data to assist interpretation.

To test the prediction that exotic plants exert stronger effects on smaller-bodied reptile species, reptile abundance data were separately analysed in three ways: (i) total reptile abundance, (ii) abundance of the smallest bodied reptiles (*Lampropholis* spp.) and (iii) abundance of all other larger-bodied (non-*Lampropholis* spp.) species. In the Lantana study, *L. delicata* was the only *Lampropholis* species recorded. In the Bitou study *L. delicata* and *L. guichenoti* were recorded. Mean adult snout-vent lengths (SVL) of *L. delicata* and *L. guichenoti* are 51 mm and 48 mm respectively (Wilson & Swan, 2010). In both the Lantana and Bitou studies, the next smallest species recorded was the scincid lizard *Saiphos equalis*, a species attaining an average adult SVL of 75 mm (Wilson &Swan, 2010), approximately 50% larger than either *L. delicata* or *L. guichenoti*.

3.2.4 Amphibian species richness and abundance

Low numbers of amphibians were recorded in both the Lantana and Bitou studies. In the Lantana study, only two frogs were detected by active searches. A single individual of *Crinia signifera* was recorded from the LC2 Belmont control site in the autumn 2010 survey, with a second recorded from the same site in the summer 2011 survey. In the Bitou study, only two *C. signifera* were recorded. One from the BC1 Kurnell control site in the autumn 2010 survey and one from the BC2 Kurnell control site in the summer 2011 survey. While it is interesting to note that no frogs were recorded from invaded sites in either the Lantana or Bitou studies, the total numbers of frogs recorded are insufficient to permit any detailed statistical analysis or make

valid comparisons between control and invaded sites. For the remainder of this chapter I focus on the reptile data.

3.3 Results

3.3.1. Lantana study

Total reptile abundance was significantly lower in invaded sites than in uninvaded sites (Table 3.3; Fig. 3.7a). Indeed, reptile abundance in invaded sites was approximately half that of uninvaded sites. This was the case in each sampling period with no significant effect of Time detected, nor was there was any significant interaction between Condition and Time. When the small-bodied *L. delicata* was considered on its own, its abundance was significantly lower in invaded vegetation and all other factors in the general linear model were non-significant (Table 3.3; Fig. 3.7b). There was no effect of Condition or any other factors in the general linear model on the abundance of all species without *L. delicata* (Table 3.3; Fig 3.7c), indicating that the smallest species present was driving the difference in reptile abundance between invaded and uninvaded vegetation.

There was no significant effect of Condition on reptile species richness (Fig. 3.8; Table 3.3). No significant effects of Time or interaction between Condition and Time were detected.

Table 3.3. GLM results for reptile abundance and species richness in relation to invasion of dry sclerophyll forest by *Lantana camara*. Significant *P* values are in bold. 'Condition' = invaded or uninvaded, 'Time' = autumn, spring or summer.

	Condition		Time		Condition*Time	
Abundance	$F_{1,22}$	*P*	$F_{2,22}$	*P*	$F_{2,22}$	*P*
Total	13.41	**< 0.01**	0.12	0.89	0.26	0.77
Lampropholis delicata	11.31	**< 0.01**	0.11	0.90	0.13	0.88
Total without *L. delicata*	0.02	0.89	0.23	0.78	1.14	0.34
Species richness	0.02	0.89	1.22	0.31	0.46	0.64

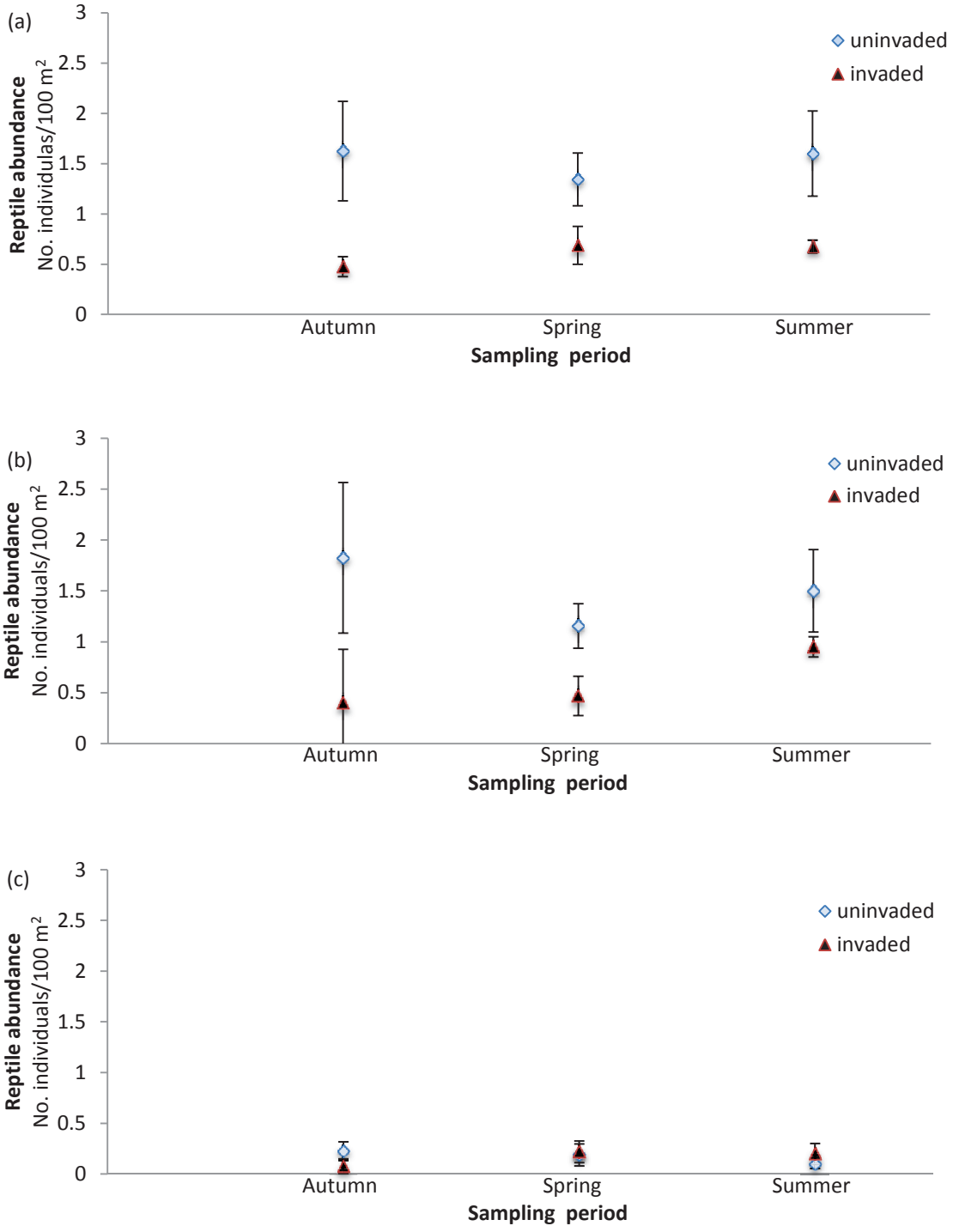

Fig. 3.7. Mean abundance/100 m^2 (± SE) of (a) all reptiles, (b) *Lampropholis delicata*, (c) all reptile species excluding *Lampropholis delicata* compared between sites of dry sclerophyll forest invaded by *Lantana camara* and uninvaded sites.

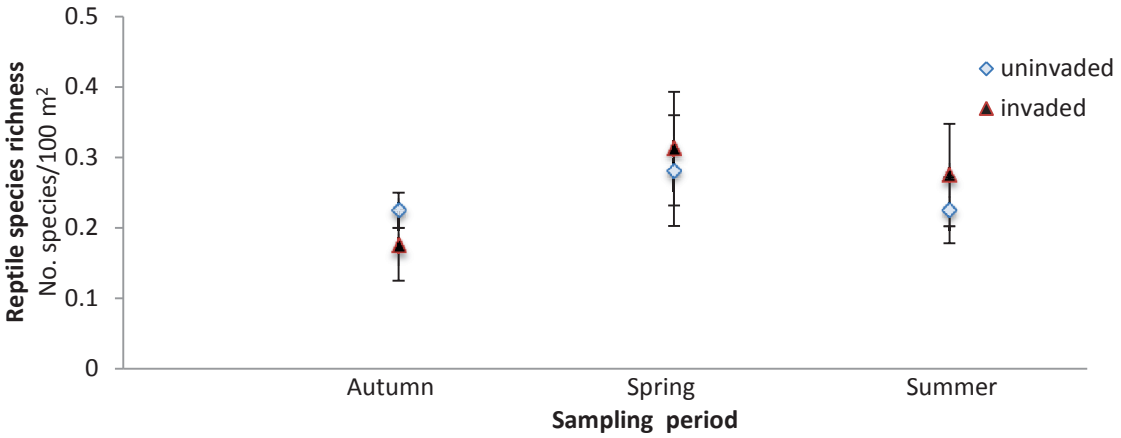

Fig 3.8. Mean reptile species richness/100 m^2 (± SE) compared between sites of dry sclerophyll forest invaded by *Lantana camara* and uninvaded sites

The composition of reptile assemblages was comparatively quite similar in invaded and uninvaded vegetation (Table 3.4). A total of eight species were recorded in uninvaded and seven in invaded vegetation with five species in common (Table 3.4). *Amphibilurus muricatus* and *Lampropholis delicata* were the predominant species in both habitat conditions (Table 3.4). Three species were recorded only in uninvaded vegetation and not in invaded vegetation (*Demansia psammophis psammophis*, *Acritoscincus platynotum* and *Varanus varius*). Two species only were recorded in invaded and not uninvaded vegetation (*Bellatorias major* and *Anamalopus swansoni*). Differences in species composition between the two habitats generally comprised less abundant species (1-2 individuals recorded). *Bellatorias major* was the only exception with five individuals recorded from invaded vegetation and none recorded in uninvaded vegetation. These compositional patterns are considered further in the Discussion (section 3.4).

Table 3.4. Total abundance of reptile species compared between sites of dry sclerophyll forest invaded by *Lantana camara* and uninvaded sites in Autumn 2010, Spring 2010 and Summer 2011. [1] = five sites sampled, [2] = four sites sampled.

Family	Species	Invaded			Uninvaded		
		Autumn[1]	Spring[2]	Summer[1]	Autumn[1]	Spring[2]	Summer[1]
Agamidae	*Amphibolurus muricatus*	1	2	2	5	4	
Elapidae	*Demansia psammophis psammophis*					1	2
	Hemiaspis signata			1			1
Scincidae	*Anomalopus swansoni*			1			
	Acritoscincus platynotum				1		
	Bellatorias major		2	3			
	Ctenotus robustus	2		1	2		
	Lampropholis delicata	17	15	19	55	35	50
	Saiphos equalis		3			1	
Varanidae	*Varanus varius*				1		1

3.3.2 Bitou study

There was no significant effect of Condition on total reptile abundance (Table 3.5; Fig. 3.9a), nor any significant effect of Time or interaction between Condition and Time.

Considering *Lampropholis* spp. separately, there was no significant effect of Condition on abundance (Table 3.5; Fig. 3.9b). There was also no significant effect of Condition on abundance of all reptile species excluding *Lampropholis* spp. (Table 3.5; Fig. 3.9c). There were no significant effects of Time and no significant interactions between Condition and Time for *Lampropholis* spp. or all reptile species excluding *Lampropholis* spp. (Table 3.5).

There was no significant effect of Condition on reptile species richness (Table 3.5; Fig. 3.10). No significant effects of Time or interaction between Condition and Time were detected.

Table 3.5. GLM results for reptile abundance and species richness in relation to invasion of coastal heathland by *Chrysanthemoides monilifera* ssp. *rotundata*. 'Condition' = invaded or uninvaded, 'Time' = autumn, spring or summer.

	Condition		Time		Condition*Time	
Abundance	$F_{1,20}$	*P*	$F_{2,20}$	*P*	$F_{2,20}$	*P*
Total	0.11	0.75	0.09	0.91	0.12	0.89
Lampropholis spp.	0.47	0.50	0.08	0.92	0.07	0.93
Total without *Lampropholis* spp.	0.32	0.58	0.19	0.83	0.11	0.90
Species richness	1.57	0.23	0.10	0.90	0.50	0.62

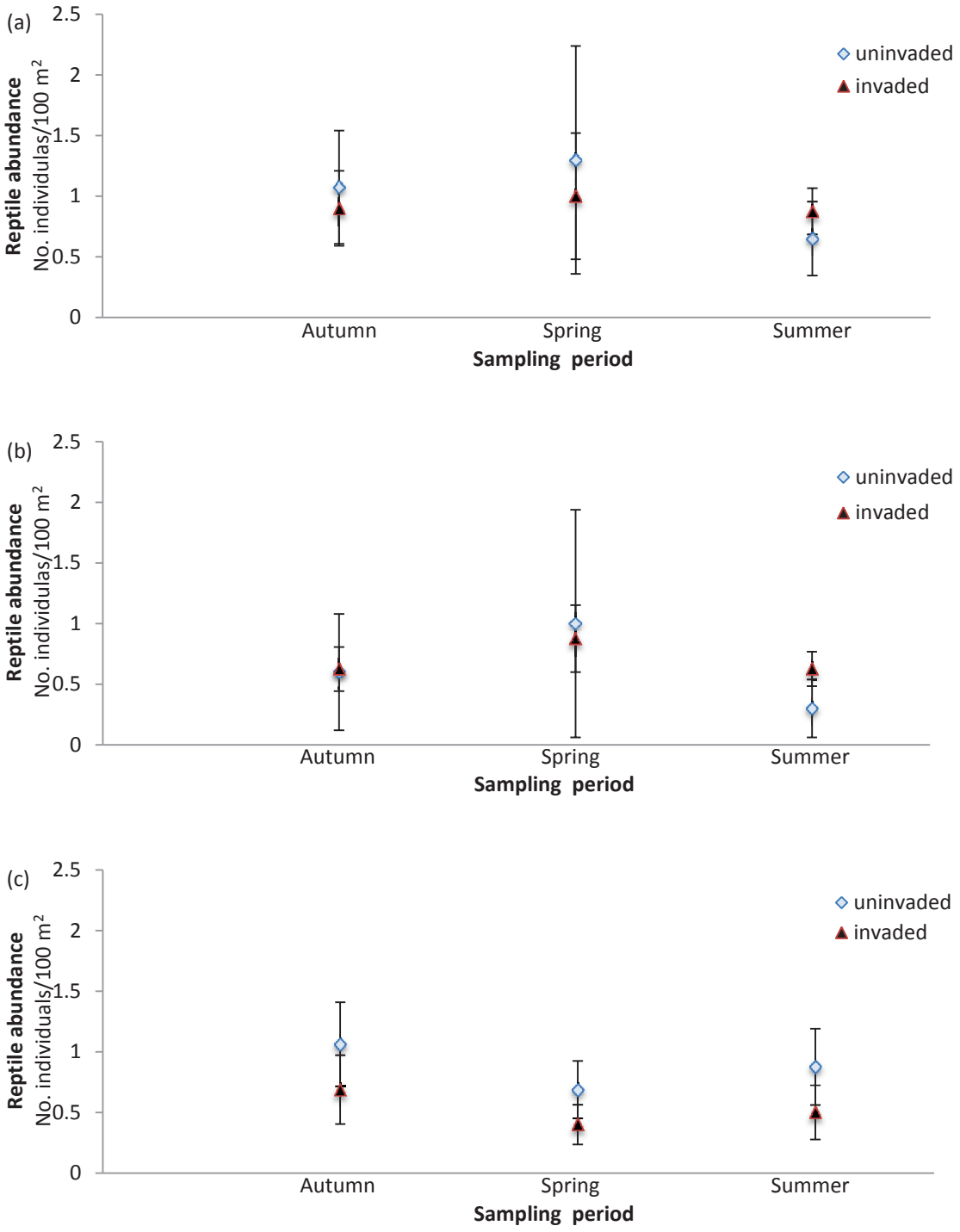

Fig. 3.9. Mean abundance/100 m^2 (± SE) of (a) all reptiles, (b) *Lampropholis* spp., (c) all reptile species excluding *Lampropholis* spp. compared between sites of coastal heathland invaded by *Chrysanthemoides monilifera* ssp. *rotundata* and uninvaded sites.

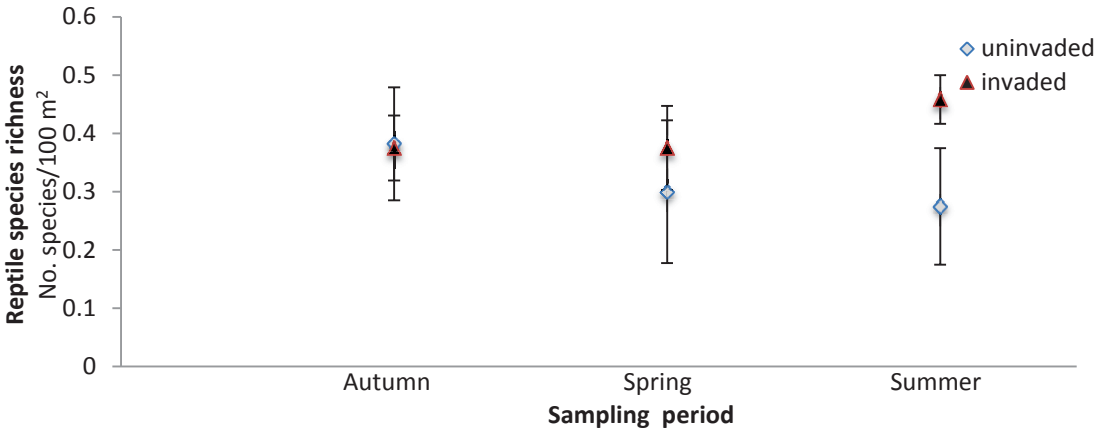

Fig. 3.10. Mean reptile species richness/100 m^2 (± SE) compared between sites of coastal heathland invaded by *Chrysanthemoides monilifera* ssp. *rotundata* and uninvaded sites.

Reptile species composition varied marginally between habitat conditions (Table 3.6). A total of nine species were recorded in invaded vegetation and seven in uninvaded vegetation with five species in common (Table 3.6). *Amphibilurus muricatus*, *Lampropholis guichenoti*, *Lampropholis delicata* and *Ctenotus taeniolatus* were the predominant species in both habitat conditions (Table 3.6). Two species were recorded only in uninvaded vegetation and not in invaded vegetation (*Hemiaspis signata* and *Tiliqua scincoides scincoides*). Four species were recorded only in invaded vegetation and not in uninvaded vegetation (*Pseudonaja textilis*, *Lialis burtonis*, *Acritoscincus platynotum* and *Saiphos equalis*). Differences in species composition between the two habitats generally comprised less abundant species with each of the species that were present in only one habitat type represented by a single individual. These compositional patterns are considered further in the Discussion (section 3.4).

Table 3.6. Total abundance of reptile species compared between sites of coastal heathland invaded by *Chrysanthemoides monilifera* ssp. *rotundata* and uninvaded sites. [1] = five sites sampled, [2] = three sites sampled

Family	Species	Invaded			Uninvaded		
		Autumn[1]	Spring[2]	Summer[2]	Autumn[1]	Spring[1]	Summer[1]
Agamidae	*Amphibolurus muricatus*	6	2	3	7	3	4
Elapidae	*Hemiaspis signata*					1	
	Pseudonaja textilis		1				
Pygopodidae	*Lialis burtonis*			1			
Scincidae	*Acritoscincus platynotum*	1					
	Ctenotus taeniolatus	3		1	6	7	6
	Eulamprus quoyii	1			4		4
	Lampropholis delicata	2	1	4	1	8	3
	Lampropholis guichenoti	19	16	9	13	12	4
	Saiphos equalis		1				
	Tiliqua scincoides scincoides					1	

3.4 Discussion

This study provides empirical evidence that life-history traits of both invading exotic plants and native reptile species interact to produce significant and negative biodiversity effects. Specifically, my findings show that small-bodied reptiles are the most sensitive to invasion by exotic plants, specifically when the invading plant species differs substantially in growth form from native plants in the invaded habitat. As expected from my predictive framework, invasion by Lantana, which represents a growth form that is either absent or not prevalent in dry sclerophyll forest, produced a strong and readily detectable impact on reptile abundance. In contrast, Bitou Bush, which represents a similar growth form to the native coastal heathland vegetation that it invades, did not have significant impacts on reptiles. As further predicted by my framework, the impacts of Lantana were exerted most strongly on the smallest bodied species present, with *Lampropholis delicata* driving the difference in total reptile abundance between invaded and uninvaded vegetation.

The different impacts of Lantana and Bitou Bush on reptiles may be due to a number of factors related to the effects of exotic plants on habitat structure and quality. Exotic plants may alter the quantity, composition and temperature of leaf litter (Valentine *et al.*, 2007), the availability of woody debris on the ground (Griffin *et al.*, 1989) and the availability of light and shade (Mott *et al.*, 2010). There is also evidence that alteration of habitat complexity and food availability due to invasion of exotic plants may alter the abundance, species richness and composition of invertebrates (Slobodchikoff & Doyen, 1977; Herrera & Dudley, 2003; Ernst & Cappuccino, 2005). This has clear implications for reptile assemblages as most lizards are invertebrate predators (Vitt & Pianka, 2007). The impacts of Lantana and Bitou Bush on habitat structure and the availability of invertebrate prey are examined in detail in Chapters 5 and 6 respectively.

Species composition was somewhat similar between invaded and uninvaded vegetation in both studies. While differences in species composition were minor and generally comprised less abundant species, they may still reflect important influences of exotic plants. Species found only in native vegetation may represent species that

have been disadvantaged by exotic vegetation at invaded sites. Species found only at invaded sites may have benefited from the presence of exotic vegetation by being able to colonise previously unsuitable habitats. In particular, the presence of *Bellatorias major* in invaded Lantana study sites raises important questions regarding exotic plants facilitating the entry of some native reptile species into habitats from which they have previously been absent. *Bellatorias major* naturally occurs in wet sclerophyll and rainforest vegetation (Cogger, 2000; Wilson & Swan, 2010), reflecting a preference for cooler and shadier conditions than those which naturally occur in dry sclerophyll forest. This natural habitat of *B. major* is declining and the species is now commonly found using Lantana and Blackberry thickets as refuge habitat (Griffiths, 2006; Wilson & Swan, 2010). The presence of *B. major* in dry sclerophyll vegetation invaded by Lantana and its absence from uninvaded dry sclerophyll vegetation provides evidence to support Chapter 2 framework predictions that exotic species may have positive impacts on some reptile species while causing negative impacts on others. Similar results have been reported with the effects of exotic pines (*Pinus* spp.) on reptile species composition. Pine plantations are cooler and receive less radiant energy than native forests (Mott *et al.*, 2010). Reptile assemblages in these pine plantations comprised mostly closed-canopy rainforest species that prefer cooler, shadier habitats in contrast to surrounding native vegetation, which supported open woodland species (Mott *et al.*, 2010). The positive impact of Lantana on *B. major* points to an important management issue associated with removal of exotic vegetation. The role of exotic plants such as Lantana in providing refuge habitat for some species whose natural habitat is declining must be weighed against the deleterious impacts on other species such as those demonstrated in this study. Decisions as to whether and how exotic plant species should be removed may need to be made on a case-by-case basis, taking into account the exotic vegetation and native fauna present at each individual site and the possible impacts of available control methods. A case study of the response of reptile assemblages to the control of an exotic plant species is presented in Chapter 4 of this thesis.

The herbicide treatment of two invaded Bitou Bush sites reduced the level of replication available in spring and summer surveys in the Bitou study. This might raise questions that differences between the impacts of Lantana and Bitou Bush detected in this study were an artefact of this difference in survey effort, however, re-analysis of reptile abundance data for the Lantana study with spring and summer survey results from two randomly selected Lantana invaded sites omitted (i.e. equivalent replication to the Bitou study) did not qualitatively alter results. Total reptile abundance and abundance of *L. delicata* remained significantly lower in Lantana invaded vegetation (see Appendix 1).

It is possible that Bitou Bush and Lantana may exert impacts on reptiles, other than those detected in this study. In particular, the framework I presented in Chapter 2 predicts that larger-bodied reptiles will become more susceptible to impacts as coverage (i.e. stand size) of exotic plants increases. Further studies utilising a variety of stand sizes at multiple spatial scales are required to test this prediction. Nevertheless, the results presented here indicate that, as predicted, the impact of exotic plants will vary depending on the life-history traits of the exotic plant and native reptile species involved.

Further work is needed to examine the response of amphibians to invasion of native vegetation by exotic plants. Amphibian numbers recorded in this study were too low to allow detailed data analysis or test framework predictions regarding the importance of exotic plant growth form and amphibian life-history traits in determining the impacts of exotic plants on amphibians. Future studies should focus on comparing frog habitats such as streams and ponds subject to exotic plant invasion with uninvaded frog habitat. This should include recording frog microhabitat usage to determine whether exotic plants are being avoided or utilised as habitat by frogs. Combining nocturnal and diurnal surveys is also recommended to increase the numbers of frogs detected. Nocturnal surveys were not practical in this study due to access authorisation constraints at a number of sites.

Nocturnal surveys would also increase the probability of detecting nocturnal reptiles. Diurnal active searches included inspection of retreat sites likely to be used by

nocturnal reptiles (beneath rocks, logs and loose bark) and resulted in detection of the nocturnal *Saiphos equalis*. It is possible, however, that some nocturnal reptiles that may have evaded detection in diurnal searches could have been recorded in nocturnal surveys.

Chapter 4: Response of a native reptile assemblage to spot-spraying of Bitou Bush, *Chrysanthemoides monilifera* ssp. *rotundata*, with glyphosate herbicide

4.1 Introduction

The exotic plant species Bitou Bush, *Chrysanthemoides monilifera* ssp. *rotundata*, is a widespread invader of coastal areas of eastern Australia (Australian Weeds Committee, 2010). Invasive Bitou Bush is listed as a Weed of National Significance in Australia as it poses a threat to a number of native plant, bird and mammal species (Coutts-Smith & Downey, 2006; French *et al.*, 2008; Winkler *et al.*, 2008). Furthermore, 'Invasion of native plant communities by *Chrysanthemoides monilifera* (Bitou Bush and Boneseed)' has been listed as a key threatening process under the Threatened Species Conservation Act 1995 (NSW Scientific Committee, 1999).

Application of the herbicide glyphosate by spot or aerial spraying is considered an effective broad-scale method of controlling Bitou Bush (DEC, 2006). The highly-diluted concentrations of glyphosate used in herbicide applications are unlikely to bioaccumulate in large quantities, with more recent formulations generally considered safe for terrestrial animals (Bayless, 2000). Nevertheless, there are concerns about the potentially deleterious effects on non-target plant and animal species of spraying weeds such as Bitou Bush with glyphosate (DEC, 2006). Considering that Bitou Bush is thought to be utilized as habitat by the Diamond Python (*Morelia spilota spilota*) and several native skink species (Winkler *et al.*, 2008), it needs to be determined whether glyphosate spraying of Bitou Bush has deleterious effects, or indeed if it has little impact, on native reptile assemblages.

In this chapter, I explore the short-term impacts of control of Bitou Bush by glyphosate on reptile assemblages. During my work examining the effects of Bitou Bush invasion on native reptile assemblages at ten sites (five invaded compared with five uninvaded, see Chapter 3) in coastal heathland vegetation in eastern Australia, unexpected spraying of the glyphosate herbicide Roundup® Biactive™ Bitou Bush occurred at two of the five invaded sites. The glyphosate spot-spraying resulted in near to 100% mortality of Bitou Bush at these two study sites. Sprayed Bitou Bush was

present as dead vegetation with little regeneration (approximately 1-2% percentage cover) of either native vegetation or Bitou Bush observed in the November 2010 (Spring) or February 2011 (Summer 2010/11) surveys. I used this unexpected application of glyphosate herbicide as an opportunity to provide a preliminary assessment of the impacts on reptiles of glyphosate spot-spraying of Bitou Bush. I employed a multiple before-after reference control-impact (M-BARCI) design (e.g. Lake, 2001) to compare reptile assemblages among uninvaded (reference) sites, invaded (control) sites and invaded and sprayed (impact) sites before and after spot-spraying. Since this study was not initially set up to provide a comprehensive assessment of the response of native reptile assemblages to glyphosate spraying of Bitou Bush, I interpret my findings cautiously and point to ways in which future large-scale manipulative experiments might address the broader issue of potential collateral damage to native biodiversity as a result of the use of glyphosate to manage a range of weed species.

4.2 Methods

4.2.1 Site descriptions and experimental design

Prior to the unexpected glyphosate spot-spraying, my initial study design consisted of a total of ten sites, with five uninvaded sites and five sites invaded by Bitou Bush. See chapter 3 for details of site locations, study plots (section 3.2.1) and reptile sampling methods (section 3.2.2). Soon after completion of the autumn 2010 survey, two invaded sites (BI1 Kurnell and BI4 La Perouse) were subjected to glyphosate herbicide treatment of Bitou Bush by the NSW National Parks and Wildlife Service in late May to early June. The revised experimental design used in the present study thus consisted of five uninvaded (reference) sites (BC1 Kurnell 1, BC2 Kurnell 2, BC3 Greenhills Reserve, BC4 La Perouse and BC5 Malabar Headland), three invaded (control) sites (BI2 Greenhills Reserve, BI3 Charlotte Breen Reserve and BI5 Malabar Headland) and the two invaded and sprayed (impact) sites. All sites were surveyed in April 2010 (autumn), before glyphosate spot-spraying and after spot-spraying in November 2010 (spring)

and February 2011 (summer). Reptile abundance and species richness at sprayed (impact) sites were compared with the unsprayed, invaded (control) sites and the uninvaded (reference) sites.

4.2.2 Statistical analysis

Reptile abundance and species richness data were analysed using separate generalised linear models (GenLM) in SPSS v.20. This type of model is robust to the unbalanced design necessitated in this study. 'Condition' was a fixed factor with three levels (uninvaded, invaded, sprayed). 'Time' was a fixed factor with three levels (autumn, spring, summer) and an interaction term for Condition x Time was included in the models. In the analyses, the emergence of a significant Condition x Time interaction, linked to lower reptile abundance and/or richness in the sprayed sites after spraying, would indicate that glyphosate spot-spraying was associated with declines in reptile biodiversity. In contrast, no significant Condition x Time interaction in both models would indicate that glyphosate spot-spraying of Bitou Bush did not have a significant effect on either reptile abundance or species richness. I used Wald Chi-square tests for tests of statistical significance. Data were checked for normality using Kolmogorov-Smirnov tests and a normal probability distribution and identity link function were specified in the models.

4.3 Results

There was no significant effect of Condition (Wald χ^2_2 = 0.45, P = 0.80) or Time (Wald χ^2_2= 0.02, P = 0.99) on reptile abundance (Fig. 4.1). There was no significant Condition x Time interaction (Wald χ^2_4= 1.37, P = 0.85), indicating a non-intrusive effect of glyphosate spot-spraying of Bitou Bush on reptile abundance.

There was no significant effect of Condition (Wald χ^2_2 = 4.16, P = 0.13) or Time (Wald χ^2_2 = 0.68, P = 0.71) on reptile species richness (Fig. 4.2). I also found that there was no significant Condition x Time interaction (Wald χ^2_4 = 3.21, P = 0.52), indicating

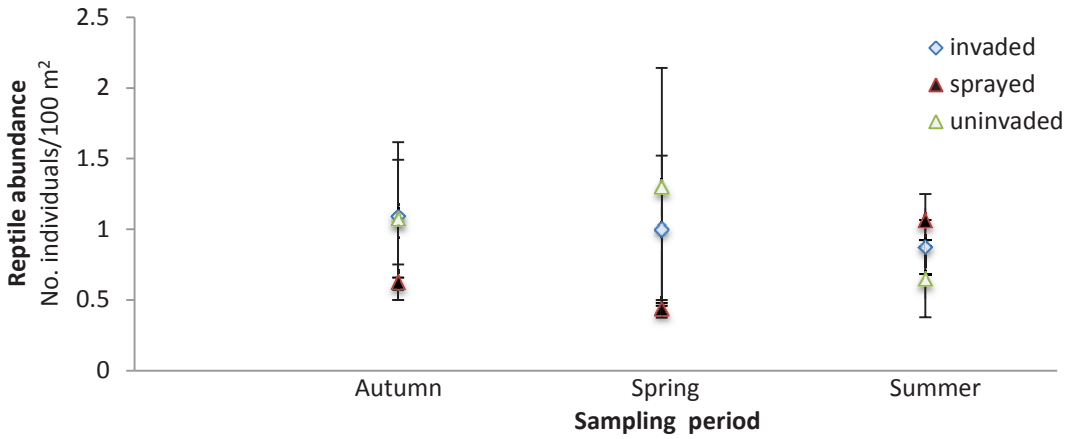

Fig. 4.1. Mean reptile abundance/100 m^2 (± SE) at uninvaded, invaded and sprayed sites, before (autumn 2010) and after (spring 2010 and summer 2011) application of glyphosate herbicide to Bitou Bush (*Chrysanthemoides monilifera* ssp. *rotundata*) at sprayed sites

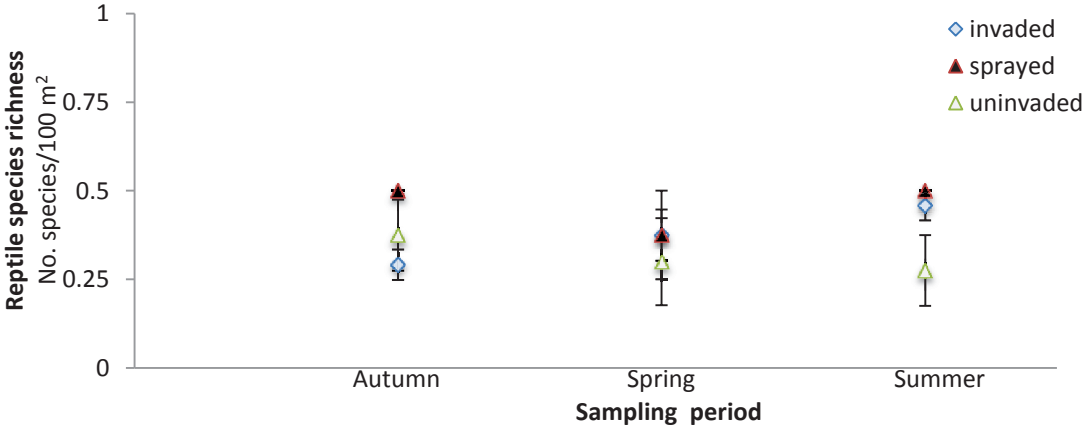

Fig. 4.2. Mean reptile species richness/100 m^2 (± SE) at uninvaded, invaded and sprayed sites, before (autumn 2010) and after (spring 2010 and summer 2011) application of glyphosate herbicide to Bitou Bush (*Chrysanthemoides monilifera* ssp. *rotundata*) at sprayed sites.

Table 4.1. Reptile species found in Bitou Bush (*Chrysanthemoides monilifera* ssp. *rotundata*) before and after herbicide spraying ('Sprayed') in autumn 2010 compared with 'Unsprayed' Bitou Bush and 'Uninvaded' vegetation. + = present; - = absent.

Family	Species	Before spraying			After spraying		
		Sprayed	Invaded	Uninvaded	Sprayed	Invaded	Uninvaded
Agamidae	*Amphibolurus muricatus*	+	+	+	+	+	+
Elapidae	*Hemiaspis signata*	-	-	-	+	-	+
	Pseudonaja textilis	-	-	-	-	+	-
Pygopodidae	*Lialis burtonis*	-	-	-	-	+	-
Scincidae	*Acritoscincus platynotum*	+	-	-	+	-	-
	Ctenotus taeniolatus	+	-	+	+	+	+
	Eulamprus quoyii	+	-	+	-	-	+
	Lampropholis delicata	+	+	+	+	+	+
	Lampropholis guichenoti	+	+	+	+	+	+
	Tiliqua scincoides scincoides	-	-	-	-	-	+
	Saiphos equalis	-	-	-	-	+	-

that glyphosate spot-spraying of Bitou Bush did not have a significant effect on reptile species richness.

Reptile species composition was remarkably similar among habitat conditions before and after spraying (Table 4.1). *Amphibilorus muricatus*, *Lampropholis guichenoti*, and *Lampropholis delicata* were were commonly found in all three site conditions before and after spraying. *Ctenotus taeniolatus* was absent only from invaded sites in pre-spraying surveys but was common in all other site conditions at all sampling times. *Eulamprus quoyii* was recorded at uninvaded sites in pre-spraying and post-spraying surveys but was only recorded in pre-spraying surveys at sprayed sites. *Hemiaspis signata* was absent from sprayed sites prior to spraying but present after spraying. Importantly, species composition of sprayed sites changed little between surveys conducted before and after spraying with only one species, *Eulamprus quoyii* recorded pre-spraying but absent from post-spraying surveys and one species, *Hemiaspis signata* absent pre-spraying but present in post-spraying surveys.

4.4 Discussion

Given the opportunistic nature of my study and the small number of impact sites (two in total), I cautiously interpret my results to generate a preliminary finding that the spot-spraying of Bitou Bush with glyphosate appears not to have a deleterious effect on reptile abundance, species richness or composition at seven and ten months following herbicide application. Clearly, it will be of great value to utilize a larger number of impact sites in future to examine the impacts of glyphosate on reptile as well as other faunal and floral assemblages. Nevertheless, I believe my finding is probably a reliable indication of the effects of glyphosate on reptile assemblages for three reasons.

First, survey efforts within each site were comprehensive and more than adequate to obtain robust measures of the structure of reptile assemblages. The survey areas of 800 m^2 for large sites and 400 m^2 for small sites are comparable with other published studies that have described exotic plant influences on reptile assemblages (e.g. Barrows and Allen, 2010). Second, my finding is consistent with

previous work (Lindsay & French, 2004a) that found no effect of spraying Bitou Bush with glyphosate on the abundance or composition of leaf-litter invertebrates. Third, when I initially designed the larger study to examine invasive impacts of Bitou Bush on native reptiles, I predicted that there would be no significant difference in reptile assemblages between invaded and uninvaded sites based on the conceptual framework presented in Chapter 2. I predicted that in systems where an invasive plant species is similar in growth form to the invaded habitat, there should not be substantial impacts on resident reptile assemblages. Habitat surveys (see Chapter 5) of the coastal heathland sites used in the present study, indicated that invading Bitou Bush does not differ substantially in growth form from native shrub species in the vegetation (e.g. *Acacia longifolia* var. *sophorea*, and *Banksia* spp.).This contrasts with a previous study that found Bitou Bush invasion was associated with cooler and darker leaf-litter conditions and higher soil moisture when compared to native vegetation (Lindsay & French, 2004b). An important distinction between the two studies is the extent of Bitou Bush cover. Bitou Bush averaged approximately 40% cover at invaded sites in my investigation whereas the minimum cover of Bitou Bush reported by Lindsay and French (2004b) was 70%. Increased cover of exotic plants is associated with greater levels of habitat modification (see Chapter 2). Thus, the finding in the present study that there are no substantial differences in reptile assemblages between uninvaded and invaded sites is not surprising. Furthermore, the fact that I then found no differences in reptile assemblages among uninvaded, invaded and sprayed sites before and after spraying is to be expected if glyphosate is not having a deleterious effect on the abundance, richness and composition of reptiles.

Considering together the three issues outlined above, I believe that this study provides reliable preliminary evidence of the non-intrusive effects of spot-spraying Bitou Bush with glyphosate. Nevertheless, more work needs to be done to provide a larger body of evidence for non-intrusive impacts of glyphosate in general. I would not recommend basing management decisions on the outcomes of this study alone, but rather, these findings can be used to develop more strategic analyses of glyphosate impacts.

It is possible, for instance, that control of Bitou Bush may reduce reptile abundance during particularly short time frames (i.e. less than six months) when the impacts may be felt more intensely. Bitou Bush provides cover to protect some small skink species from predators which include introduced cats and dogs (Winkler *et al.*, 2008). Larger, planned studies with increased replication are needed to determine whether reptile abundance is reduced within six months of spraying.

The relatively small number of reptiles encountered in surveys reflects the size of sprayed Bitou Bush patches. While use of larger sites may have increased reptile numbers that I observed, the use of longer transects at the unsprayed sites would have resulted in confounding the observation of effects of glyphosate spot-spraying with the effects of increasing native vegetation and unsprayed Bitou Bush. Consequently, while my results are relevant for spot-spraying of smaller Bitou Bush patches, I cannot extrapolate my results to larger spray events such as might occur in aerial spraying of large stands.

Further studies are also needed to determine the response of reptiles to Bitou Bush control that does not use glyphosate such as physical removal, burning and biological control. This would allow the efficacy and impacts of available control methods to be compared. The longer-term response of reptiles to Bitou Bush control also requires further study. The period covered by this investigation represents only a single reptile breeding season (Heatwole & Taylor, 1987). Longer-term investigations are needed to determine the ongoing response of reptiles to Bitou Bush control over several years. This work should be a priority, given the increasing need to control Bitou Bush due to its invasive spread and the detrimental impacts of this spread on other native species of plants, birds and mammals (Coutts-Smith & Downey, 2006).

Chapter 5: Impacts of Lantana (*Lantana camara*) and Bitou Bush (*Chrysanthemoides monilifera* ssp. *rotundata*) on reptile habitat

5.1 Introduction

The composition and structure of reptile assemblages are influenced by habitat structure and heterogeneity (Pianka, 1967; Heatwole & Taylor, 1987). These habitat features are in turn influenced by vegetation structure (Heatwole & Taylor, 1987). Exotic plant invasion can substantially change vegetation structure and the extent of change is related to the growth form of the invading species (Grice, 2004). Thus, invasion of native vegetation by exotic plants has the potential to alter the suitability of habitat for reptiles. As predicted in Chapter 2, exotic plant species exhibiting novel growth forms or structural features will exert stronger and more rapid influences on reptiles than species that replicate existing plant growth forms and structural features.

In addition to changing the vegetation structure of invaded communities, exotic plants may also alter the quantity, composition and temperature of leaf-litter (Valentine *et al.*, 2007), the availability of woody debris on the ground (Griffin *et al.*, 1989) and the availability of light and shade (Mott *et al.*, 2010). All of these changes have the potential to influence reptile assemblages given that they can all lead to substantial changes in reptile habitat conditions.

In Chapter 3 I demonstrated that Lantana (*Lantana camara*) and Bitou Bush (*Chrysanthemoides monilifera* ssp. *rotundata*) differed in their impacts on reptile abundance. Lantana invasion of dry sclerophyll forest was associated with reduced reptile abundance (particularly the abundance of small-bodied reptile species), while invasion of coastal heathland by Bitou Bush was not. Based on these results and a preliminary assessment of the impacts of Lantana and Bitou Bush on habitat structure (see Chapter 3, Figs 3.1, 3.2), I hypothesised that Lantana modifies reptile habitat within dry sclerophyll forest more strongly than Bitou Bush modifies coastal heathland habitat for reptiles. In this chapter, I present the results of fieldwork conducted to test this hypothesis. Specifically, I compared quantitatively a range of habitat traits between invaded and uninvaded sites for both Lantana and Bitou Bush. For the Bitou

Bush system, I did not expect to see significant differences in habitat characteristics between invaded and uninvaded sites. However, given my earlier observations of significant differences in reptile assemblages as a result of Lantana invasion, I tested the following predictions for differences in habitat traits between invaded and uninvaded sites in the Lantana system:

(1) Lantana invasion of dry sclerophyll forest will be associated with significant changes in vegetation structure; in particular Lantana will increase the percentage cover of understorey vegetation when compared with uninvaded dry sclerophyll forest. Bitou Bush invasion of coastal heathland will not be associated with significant changes in vegetation structure.

(2) Levels of solar radiation reaching the ground will be significantly lower in sites of dry sclerophyll forest invaded by Lantana than in uninvaded sites. Levels of solar radiation reaching the ground will not differ significantly between sites of coastal heathland invaded by Bitou Bush and uninvaded sites.

(3) Leaf-litter temperatures will be cooler in sites of dry sclerophyll forest invaded by Lantana than in uninvaded sites. Leaf-litter temperatures will be similar between sites of coastal heathland invaded by Bitou Bush and uninvaded sites.

5.2 Methods

5.2.1 Site descriptions and experimental design

The impacts of Lantana (Lantana study) and Bitou Bush (Bitou study) on reptile habitat were studied at the same sites used to investigate impacts of these exotic plant species on reptile assemblages (see Chapter 3 for location details and descriptions of study sites, section 3.2.1).

5.2.2 Habitat structure and leaf-litter characteristics

For both the Lantana and Bitou studies, a number of vegetation and leaf-litter characteristics were surveyed immediately following reptile sampling in Autumn 2010 along the same permanent transects used for reptile surveys; i.e. a transect was located 2.5 m from the vegetation edge with further transects at 15 m intervals. Four 2 m radius sampling areas were established per transect with the first area located 2.5 m from the start of the transect and the remaining sampling areas at 15 m intervals along the transect. Four transects were used in large plots (Fig. 5.1) and two in small plots (Fig. 5.2). Habitat variables were assessed using methods similar to those previously employed to assess the impacts of exotic plants on habitat for birds (Cantlay, 2006) and reptiles (Mott *et al*., 2010).

In each sampling area I made visual estimates of canopy height in metres and percentage canopy projected foliage cover using the canopy cover estimation chart of Hnatiuk *et al*. (2009) as a guide. Canopy thickness was estimated in metres by subtracting the minimum canopy height from the maximum canopy height. Understorey height was estimated in metres and understorey projected foliage cover estimated as a percentage. Shrub cover, ground vegetation cover (including grasses), log cover, stump cover, bare ground and target exotic plant species (Lantana or Bitou Bush) cover and were also estimated as percentages. Leaf-litter composition was estimated visually as the percentage of non-native leaf-litter in each sampling area. Leaf-litter depth was measured in centimetres at three random points in each sampling area using a clear plastic ruler and the results averaged. The number of trees in each sampling area was counted and divided into size classes by estimating their diameter at breast height (DBH). In the Lantana study these size classes were < 10 cm, 10-39 cm, 40-59 cm and 69-70 cm. In the Bitou study only the < 10 cm and 10-39 cm classes were used as no trees with DBH > 39cm were recorded. DBH estimates were calibrated by comparing visual estimates of randomly selected trees in each size class with direct measurements prior to commencing sampling. Data from each sampling area were averaged to give site values.

Leaf-litter depth and composition were assessed again immediately after the completion of reptile sampling in summer 2011 to determine if there had been any significant change in leaf-litter characteristics over the course of the study. In the Bitou study, two invaded sites (BI1 Kurnell and BI4 La Perouse, see Chapters 3 and 4) were subjected to herbicide treatment of Bitou Bush by the NSW National Parks and Wildlife Service soon after the completion of the autumn 2010 survey. These sites were not used in comparisons of leaf-litter depth and composition between invaded and uninvaded vegetation summer 2011. Other habitat characteristics were not sampled again as visual inspection of sites indicated no substantial change in these characteristics (other than at sprayed Bitou Bush sites).

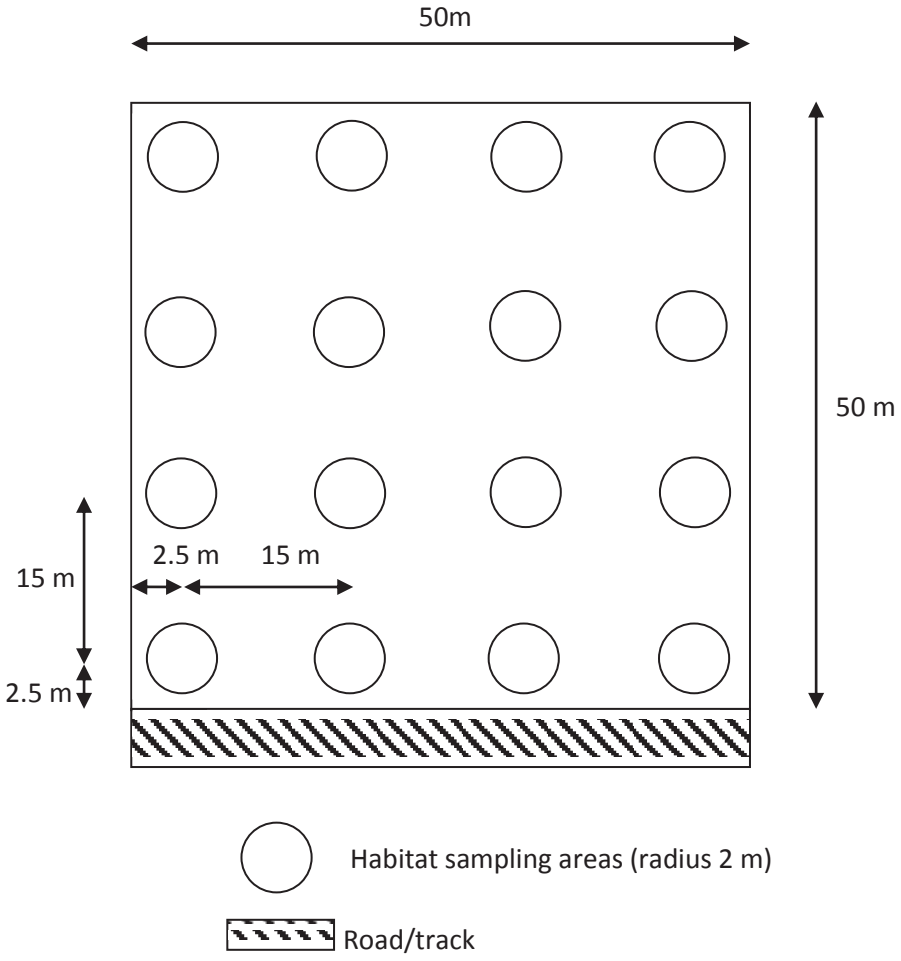

Fig. 5.1. Arrangement of habitat sampling areas in large (50 m x 50 m) study plots

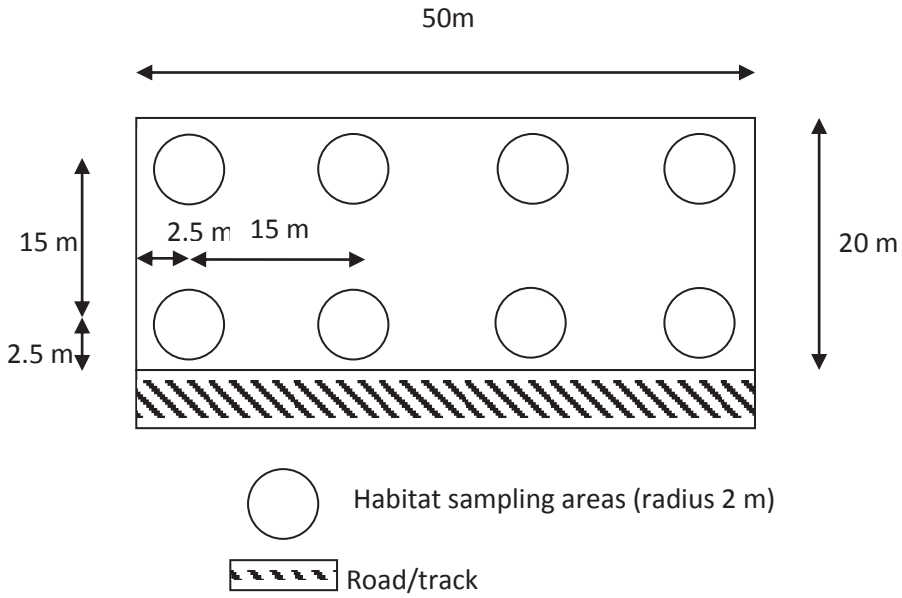

Fig. 5.2. Arrangement of habitat sampling areas in small (50 m x 20 M) study plots

5.2.3 Direct solar radiation reaching the ground

Direct photosynthetically active radiation (PAR) reaching the ground was estimated using hemispherical canopy photography. Direct solar radiation is important for reptile thermoregulation, unlike indirect solar radiation which provides insufficient radiant energy (Langkilde *et al*., 2003; Mott *et al*., 2010). A single hemispherical photograph was taken in the centre of each sampling area (Figs 5.1 & 5.2) using a Canon EOS 500D digital camera fitted with a 4.5 mm F2.8 Sigma circular fisheye lens to produce a total of 16 images per site. The camera was attached to a tripod set at a height of 50 cm above the ground. The top of the camera was orientated to magnetic north using a magnetic compass and a small spirit level was used to ensure that the camera was set level with the lens pointing directly upwards. Photographs were taken under uniform overcast conditions to ensure that no parts of the image were overexposed (Trichon *et al*., 1998; Mott *et al*., 2010). The images were analysed using Gap Light Analyzer software which measures canopy openness and calculates the solar radiation reaching the ground throughout the year taking into account the latitude, longitude, elevation, slope and orientation of sites as well average day length, average number of sunny days and the path of the sun (Frazer *et al.,* 1999; Langkilde *et al*., 2003). Values for

mean daily direct PAR calculated from each the 16 photographs taken at each site were averaged to give site values.

Canopy photography was conducted after herbicide spraying had occurred at two Bitou Bush sites in the Bitou Study. This resulted in near to 100% mortality of Bitou Bush at sprayed sites. Consequently only three Bitou Bush sites were available for the purposes of determining the amount of direct solar radiation reaching the ground in Bitou Bush invaded sites.

5.2.4 Leaf-litter temperature

For both the Lantana and Bitou studies, leaf-litter temperature was recorded at two invaded and two uninvaded sites during the autumn, spring and summer reptile surveys. Leaf-litter temperatures were recorded using Thermocron iButton™ miniature temperature data loggers placed 1-2 cm below the surface of the leaf-litter. Two data loggers were placed at the end of each transect (i.e. separated by 50 m) with a total of 8 loggers used per site. Temperatures were recorded every 30 minutes for 3 days and average temperatures calculated for invaded and uninvaded vegetation over the 72 hour period. Average temperatures during reptile survey periods (0900 to 1100 and 1500 to 1700 hours Eastern Standard Time) were also calculated. On a number of occasions several temperature loggers were found to have been disturbed by animals and left on the surface of the leaf-litter. Data from these loggers were excluded from analyses as they could not be considered a reliable record of leaf-litter temperature.

In the Lantana study, leaf-litter temperatures were recorded at the Catherine Hill Bay (LC1) and Belmont Wetland State Park (LC3) uninvaded sites and at the Nords Wharf (LI1) and Belmont Wetlands State Park (LI4) invaded sites (see Chapter 3, section 3.2.1.1 for site details) for all three survey periods. In the Bitou study, leaf-litter temperatures were recorded at the La Perouse (BC4) and Malabar Headland (BC5) uninvaded sites and La Perouse (BI4) and Malabar Headland (BI5) invaded sites during the autumn survey. The La Perouse invaded site was subjected to herbicide spraying shortly after the autumn survey. For the spring and summer surveys leaf-litter temperatures were recorded at the Kurnell 1 (BC1) and Malabar Headland (BC5)

uninvaded sites and at the Greenhills Reserve (BI3) and Malabar Headland (BI5) invaded sites (see Chapter 3, section 3.2.1.2 for site details).

5.2.5 Statistical analyses

Data for canopy height, canopy thickness, canopy cover, understorey height, understorey cover, shrub cover, ground vegetation cover, log cover, stump cover, bare ground were analysed using separate general linear models (GLMs) in SPSS v.20. 'Condition' (invaded or uninvaded) was treated as a fixed factor. Data for leaf-litter depth were analysed using a GLM with 'Condition' (invaded or uninvaded) and 'Time' (autumn 2010, summer 2011) treated as fixed factors and an interaction term for Condition x Time included in the models. Data for the percentage of non-native leaf-litter at invaded sites were analysed using a GLM with 'Time' (autumn 2010, summer 2011) treated as a fixed factor.

To ensure compliance with GLM assumptions all data were checked for normality using Kolmogorov-Smirnov tests and for homogeneity of variances using Levene's test. In the Bitou study, data for number of trees with DBH < 10 cm were normally distributed but displayed heterogeneity of variances that could not be resolved by transformation. These data were analysed using a generalised linear model (GenLM) in SPSS v.20. with a normal probability distribution and identity link function specified in the model. 'Condition' (invaded or uninvaded) was treated as a fixed factor.

Data for direct PAR reaching the ground were analysed using a GenLM in SPSS v.20. as this form of analysis is robust to the type of unbalanced design necessitated by the herbicide spraying of two invaded sites in the Bitou study. Data were checked for normality using Kolmogorov-Smirnov tests and a normal probability distribution and identity link function specified in the model. 'Condition' (invaded or uninvaded) was treated as a fixed factor.

Data for average leaf-litter temperatures during reptile survey hours (0900-1100 and 1500-1700) were analysed using a generalised linear mixed model (GLMM) in SPSS v.20. Condition (invaded or uninvaded) was a fixed factor and random sites were

nested within condition with six to eight replicate temperature loggers (depending on animal disturbance) in each site. In this respect the experimental design differs from that for other habitat variables in which sites were used as replicates. Data for each sampling period (autumn, spring and summer) were analysed separately. F tests were used for fixed factors and Wald Z tests for random factors. All data were checked for normality using Kolmogorov-Smirnov tests and normal probability distribution and identity link function specified in the model. For several GLMMs, the non-significant Site(Condition) term was removed from the model because it accounted for zero variance in the model and its inclusion led to over-parameterisation of the model.

5.3 Results

5.3.1 Lantana study

5.3.1.1 Habitat structure and leaf-litter characteristics

There was no significant effect of Condition on the total number of trees or the number of trees in each size class (Table 5.1). Nor was there any significant effect of Condition on canopy height, canopy thickness, or understorey height. Condition had no significant effect on the percentage cover of canopy projected foliage, shrubs, ground vegetation, logs, stumps or bare ground. Understorey cover was significantly higher in invaded sites than uninvaded sites (Table 5.1, Fig. 5.3). Lantana was absent from uninvaded sites and averaged approximately 35% cover at invaded sites (Fig. 5.4).

There was no significant effect of Condition ($F_{1,16}$ = 1.07, P = 0.32), Time ($F_{2,16}$ = 0.71, P = 0.41) or interaction between Condition and Time ($F_{2,16}$ = 0.14, P = 0.72) on leaf-litter depth. Exotic leaf-litter was absent from uninvaded sites and comprised approximately 30% of leaf-litter at invaded sites (Fig. 5.5). There was no significant effect of Time on the percentage of exotic leaf-litter at invaded sites ($F_{1,8}$ = 0.22, P = 0.66).

Table 5.1. GLM results for habitat structure characteristics in relation to invasion of dry sclerophyll forest by *Lantana camara*. Significant *P* values are in bold. 'Condition' = invaded or uninvaded, 'DBH' = diameter at breast height.

Habitat traits	Condition	
	$F_{1,8}$	*P*
No. Trees	1.19	0.31
No. Trees DBH <10 cm	0.32	0.59
No. Trees DBH 10 – 39 cm	2.26	0.17
No. Trees DBH 40 – 59 cm	2.58	0.15
No. Trees DBH 60-79 cm	0.18	0.68
Canopy height	0.07	0.80
Canopy thickness	0.01	0.93
Canopy % cover	0.24	0.64
Understorey height	0.78	0.40
Understorey % cover	23.80	**0.001**
Shrub % cover	0.04	0.84
Ground vegetation % cover	0.07	0.80
Log % cover	1.08	0.33
Stump % cover	1.38	0.27
Bare ground % cover	0.02	0.89

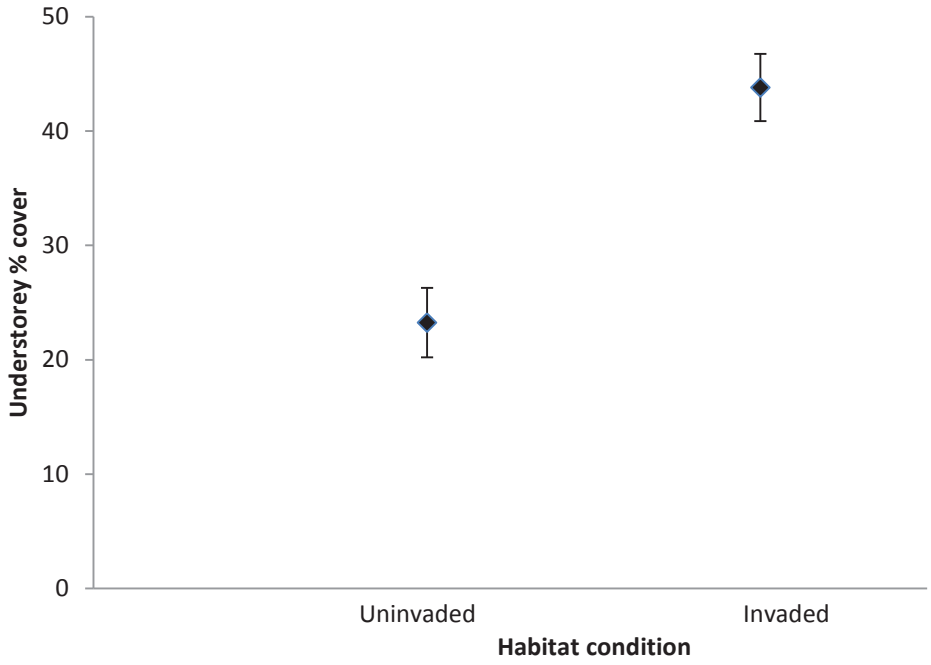

Fig. 5.3. Mean understorey projected foliage cover (± SE) compared between sites of dry sclerophyll forest invaded by *Lantana camara* and uninvaded sites.

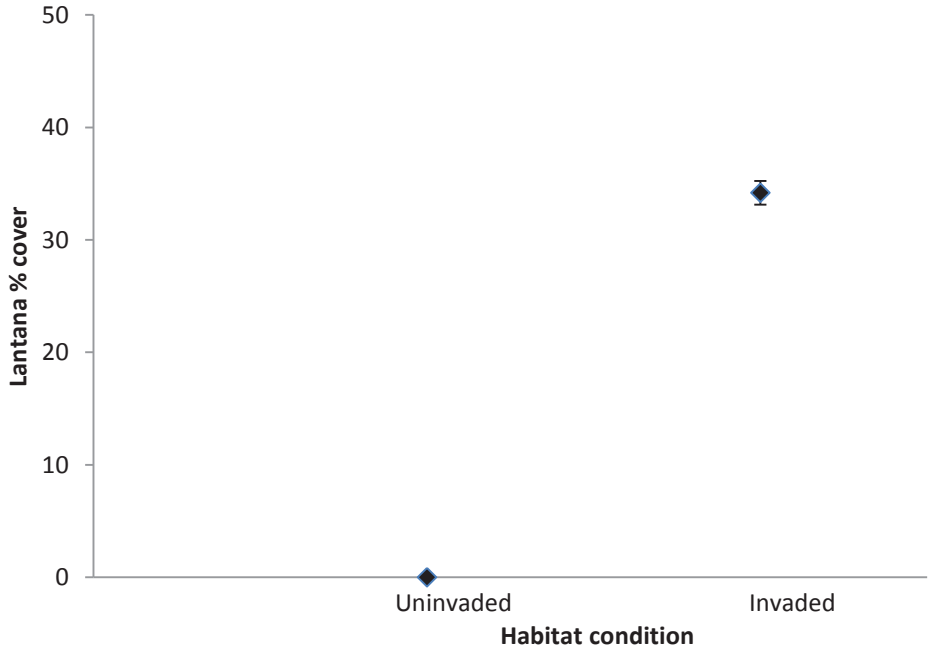

Fig. 5.4. Mean percentage cover of *Lantana camara* (± SE) compared between invaded and uninvaded dry sclerophyll forest sites.

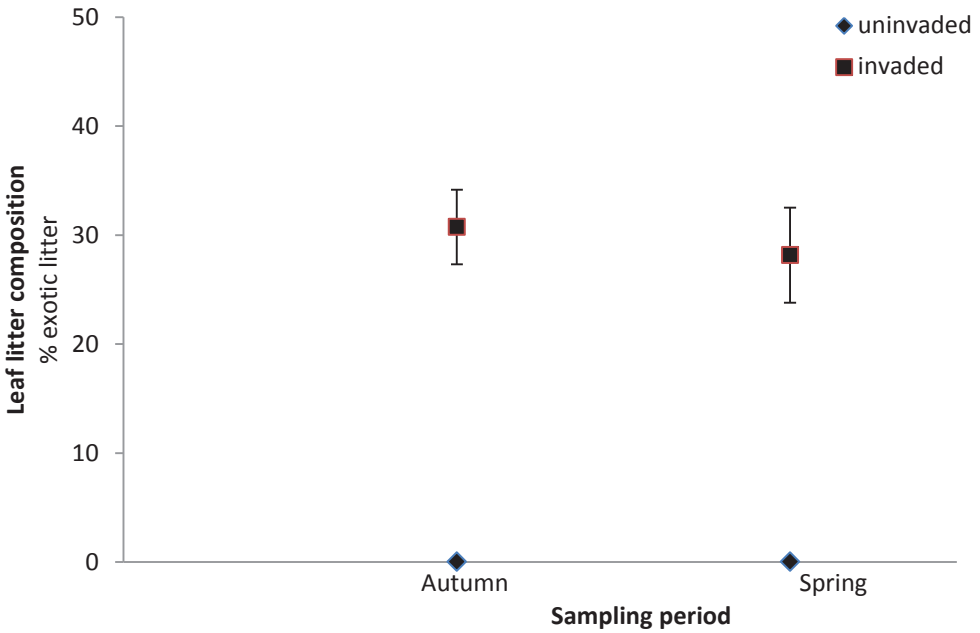

Fig. 5.5. Mean percentage of exotic leaf-litter (± SE) compared between sites of dry sclerophyll forest invaded by *Lantana camara* and uninvaded sites.

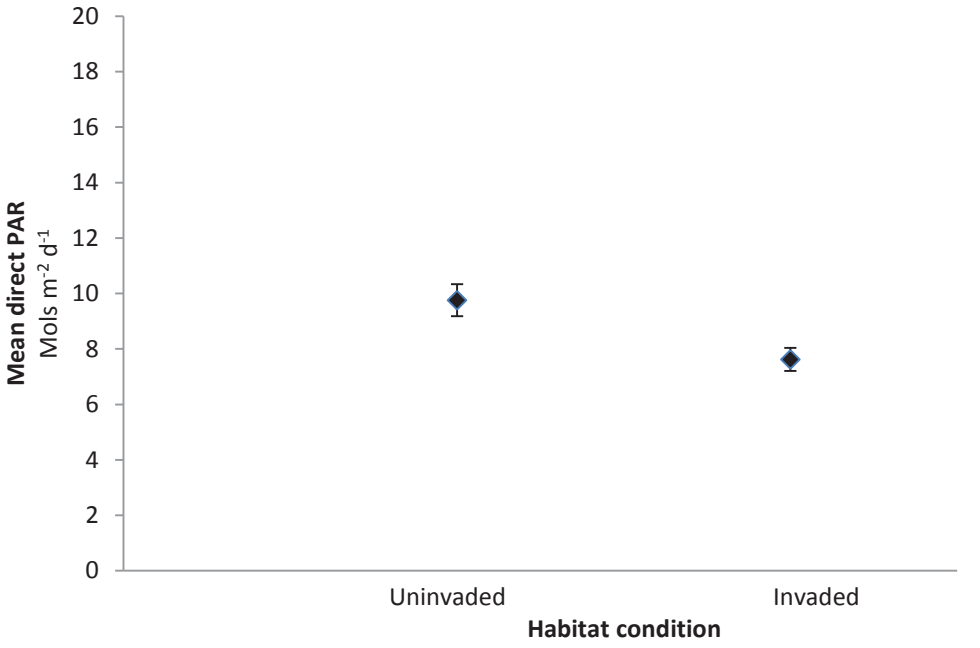

Fig. 5.6. Daily mean (± SE) direct photosynthetically active radiation (PAR) (measured as Mols $m^{-2}d^{-1}$) reaching the ground compared between sites of dry sclerophyll forest invaded by *Lantana camara* and uninvaded sites.

5.3.1.2 Direct solar radiation reaching the ground

There was a significant effect of Condition on the amount of direct solar radiation reaching the ground (Wald $\chi^2_1 = 11.24$, $P = 0.001$) with invaded habitats receiving less radiant energy than uninvaded habitats (Fig. 5.6).

5.3.1.3 Leaf-litter temperature

Leaf-litter temperatures during daylight hours were marginally higher in uninvaded sites than in invaded sites in autumn and spring (Fig. 5.7a, b), and several degrees higher in uninvaded sites in summer (Fig. 5.7c). Nocturnal leaf-litter temperatures were similar in invaded and uninvaded sites in all three seasons. Leaf-litter temperatures during reptile sampling hours followed a similar trend. Temperatures in uninvaded sites were marginally (but not significantly) warmer in autumn and spring but significantly warmer in summer (Fig. 5.8, Table 5.2).

5.3.2 Bitou study

5.3.2.1 Habitat structure and leaf-litter characteristics

There was no significant effect of Condition on the total number of trees or number of trees in the DBH 10-39 cm size class (Table 5.3). Nor was there any significant effect of Condition on the number of trees in the DBH < 10 cm size class (Wald $\chi^2_1 = 0.45$, $P = 0.50$). Condition had no significant effect on canopy height, canopy thickness, understorey height or on the percentage cover of canopy projected foliage, understorey projected foliage, shrubs, ground vegetation, logs, or bare ground (Table 5.3). Stump cover at invaded and invaded sites was 0%. Bitou Bush was absent from uninvaded sites and averaged approximately 40% cover at invaded sites (Fig. 5.9).

There was no significant effect of Condition ($F_{1,14} = 1.36$, $P = 0.26$), Time ($F_{2,14} = 0.63$, $P = 0.44$) or interaction between Condition and Time ($F_{2,14} = 0.01$, $P = 0.92$) on leaf-litter depth. Exotic leaf-litter was absent from uninvaded sites and comprised approximately 60% of leaf-litter at invaded sites (Fig. 5.10). There was no significant effect of Time on the percentage of exotic leaf-litter at invaded sites ($F_{1,6} = 0.01$, $P = 0.94$).

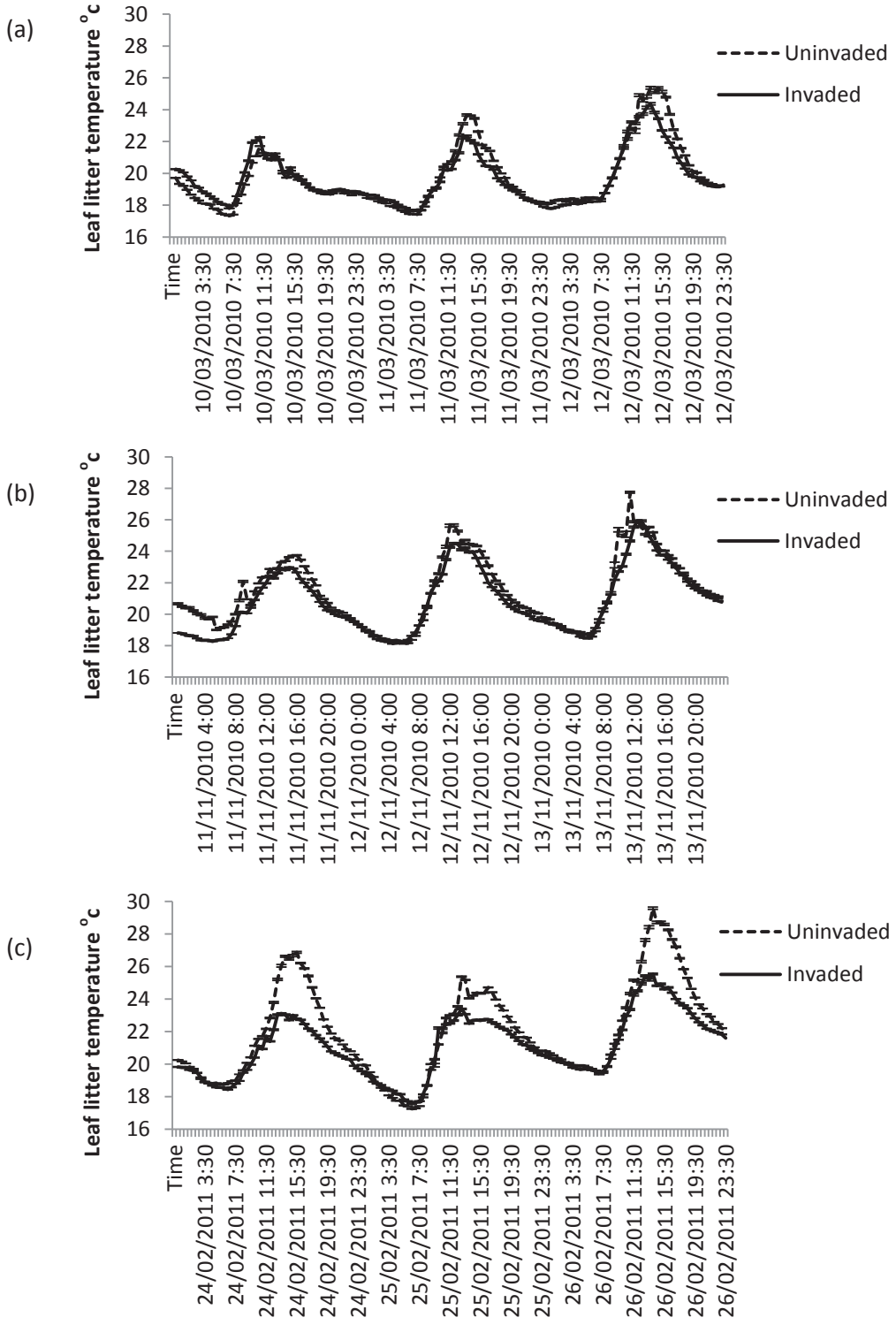

Fig. 5.7. Mean leaf-litter temperatures (± 95% CI) compared between sites of dry sclerophyll forest sites invaded by *Lantana camara* and uninvaded sites in (a) autumn 2010, (b) spring 2010, (c) summer 2011.

Table 5.2. Results of GLMMs for average leaf-litter temperature during reptile sampling hours (0900-1100 and 1500-1700) in relation to invasion of dry sclerophyll forest by *Lantana camara*. Significant *P* values are in bold. Condition = invaded or uninvaded, 'Site' is nested within 'Condition'; [1] = $F_{1,26}$, [2] = $F_{1,24}$, "-" = non-significant interaction removed from the model as its inclusion led to over-parameterisation of the model.

Season	Condition		Site(condition)	
	F	*P*	*Z*	*P*
Autumn	0.40[1]	0.53	0.82	0.42
Spring	0.53[1]	0.47	0.72	0.47
Summer	11.92[2]	**0.002**	-	-

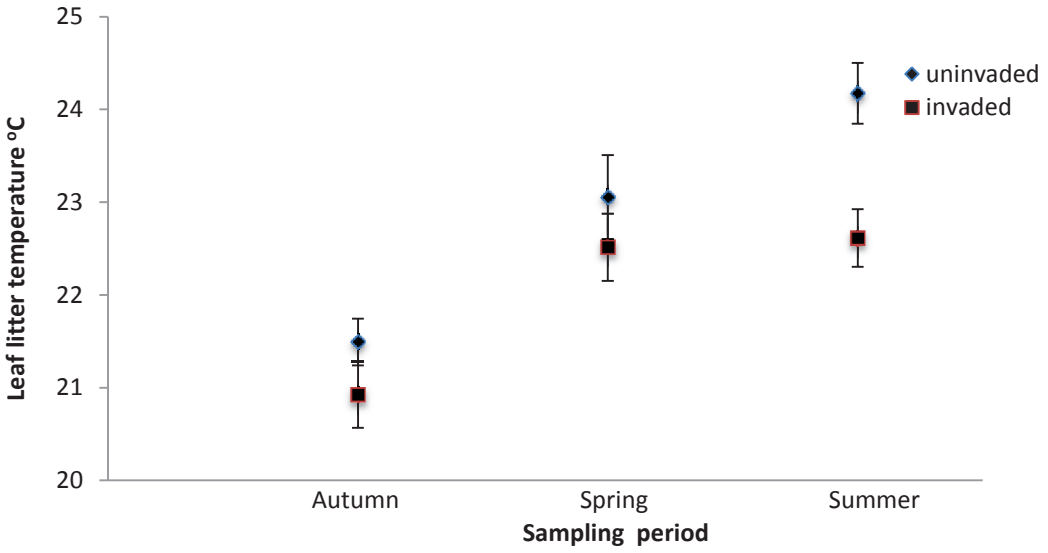

Fig. 5.8. Mean leaf-litter temperatures (± SE) during reptile sampling hours (0900-1100 and 1500-1700) compared between dry sclerophyll forest invaded by *Lantana camara* and uninvaded sites.

Table 5.3. GLM results for habitat structure characteristics in relation to invasion of coastal heathland by *Chrysanthemoides monilifera* ssp. *rotundata*. 'Condition' = invaded or uninvaded, 'DBH' = diameter at breast height.

Habitat traits	Condition	
	$F_{1,8}$	*P*
No. Trees	0.99	0.35
No. Trees DBH 10 – 39 cm	1.39	0.27
Canopy height	1.26	0.30
Canopy thickness	1.27	0.29
Canopy % cover	0.96	0.36
Understorey height	1.10	0.32
Understorey % cover	4.52	0.07
Shrub % cover	2.71	0.14
Ground vegetation % cover	0.27	0.87
Log % cover	2.33	0.17
Bare ground % cover	0.08	0.93

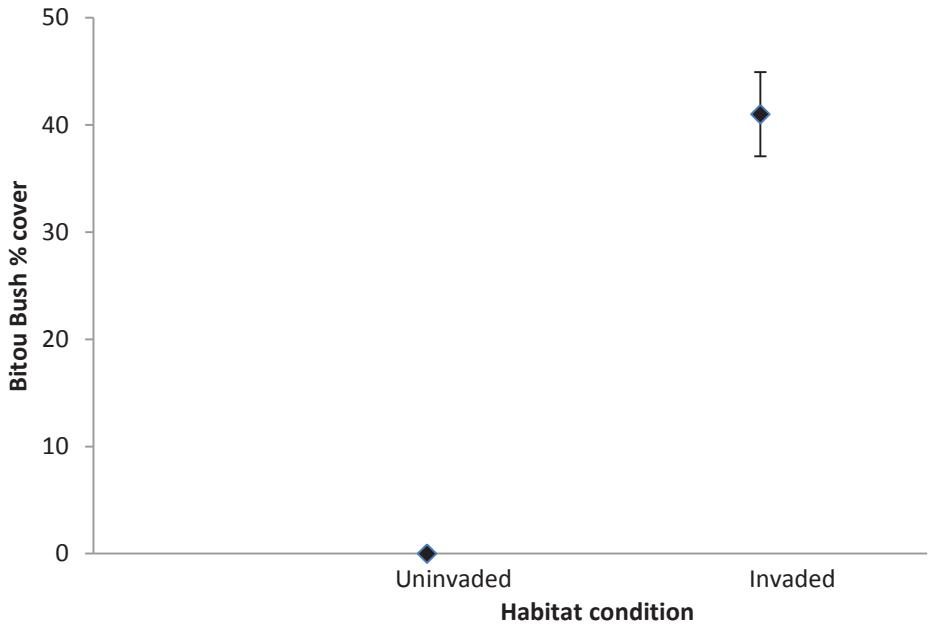

Fig 5.9. Mean percentage cover of *Chrysanthemoides monilifera* ssp. *rotundata* (± SE) compared between invaded and uninvaded coastal heathland sites.

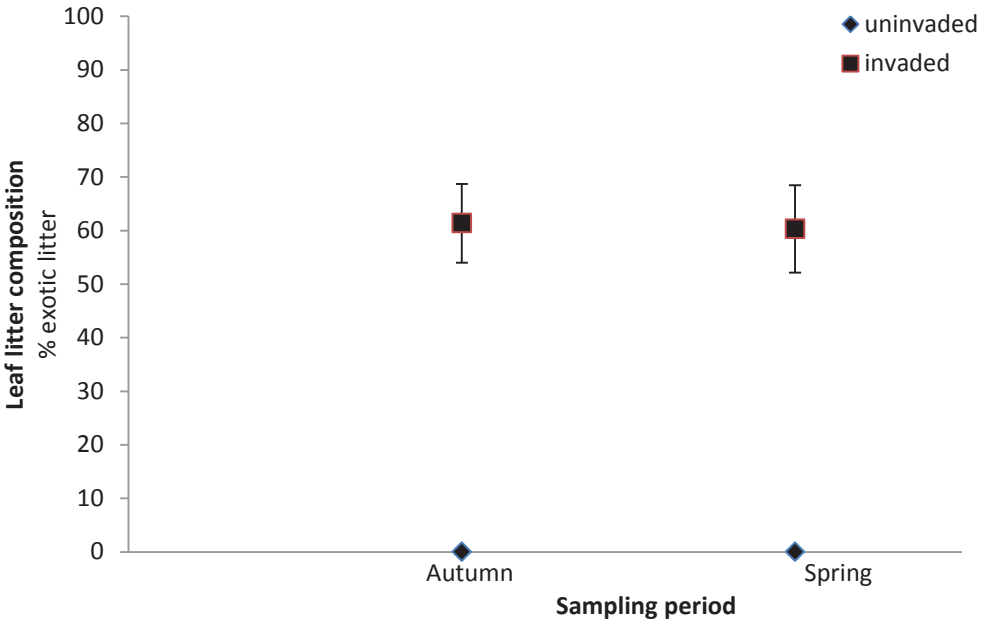

Fig 5.10. Mean percentage of exotic leaf-litter (± SE) compared between sites of coastal heathland invaded by *Chrysanthemoides monilifera* ssp. *rotundata* and uninvaded sites.

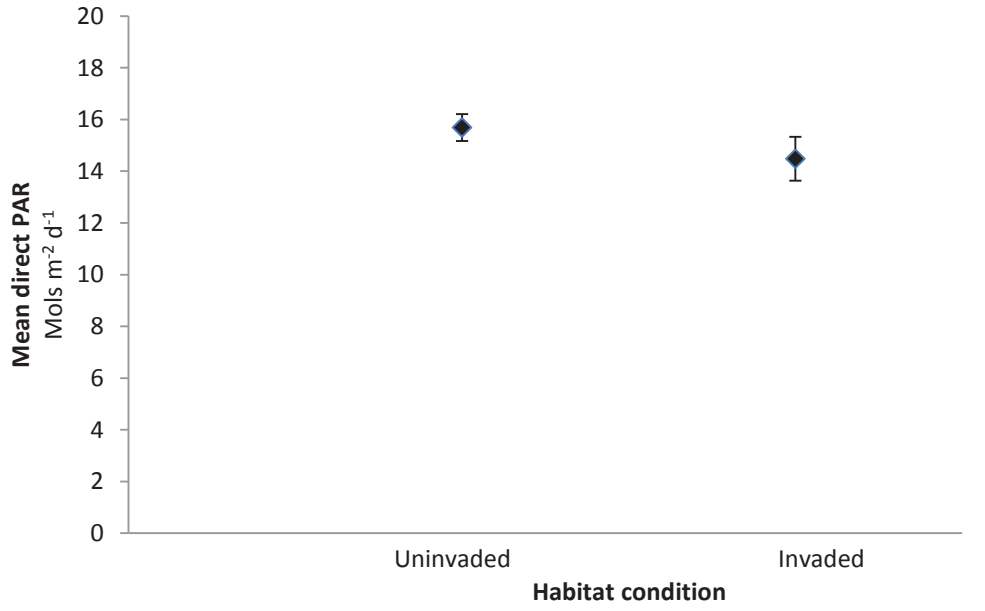

Fig. 5.11. Daily mean (± SE) direct photosynthetically active radiation (PAR) (measured as Mols $m^{-2}d^{-1}$) reaching the ground compared between sites of coastal heathland invaded by *Chrysanthemoides monilifera* ssp. *rotundata* and uninvaded sites.

5.3.2.2 Direct solar radiation reaching the ground

There was no significant effect of Condition on the amount of direct solar radiation reaching the ground (Wald $\chi^2_1 = 1.74$, $P = 0.19$) with invaded habitats receiving similar levels of radiant energy to uninvaded habitats (Fig. 5.11).

5.3.2.3 Leaf-litter temperature

Leaf-litter temperatures were similar between invaded and uninvaded habitats in autumn (Fig. 5.12a). In spring and summer morning leaf-litter temperatures were similar between habitat conditions, however, invaded sites recorded higher afternoon peak temperatures and remained warmer at night (Fig. 5.12b,c). Average leaf-litter temperatures during reptile sampling hours were generally warmer in invaded sites; however, the difference was only significant in spring. (Fig. 5.13, Table 5.4).

5.4 Discussion

Lantana and Bitou Bush differed in their impacts on the structure of reptile habitat. While Bitou Bush did not significantly alter vegetation structure of coastal heathland, Lantana invasion of dry sclerophyll forest was associated with significantly greater understorey cover when compared with uninvaded sites. These observed differences in the effects of Lantana and Bitou Bush on reptile habitat are correlated with the differences in their effects on reptile abundances. Where I observed a significant decline in reptile abundances in sites invaded by Lantana, I also observed a significant shift in habitat characteristics.

The increased understorey cover associated with Lantana invasion was reflected in lower levels of direct radiant energy reaching the ground and generally cooler diurnal leaf-litter temperatures. It is interesting to note that the difference in leaf-litter temperatures between invaded and uninvaded sites was greatest in summer, when ambient temperatures were highest. This indicates that overshadowing of habitat by Lantana limits the maximum temperatures attainable in invaded habitats and that the effects are strongest in conditions that would otherwise correspond to

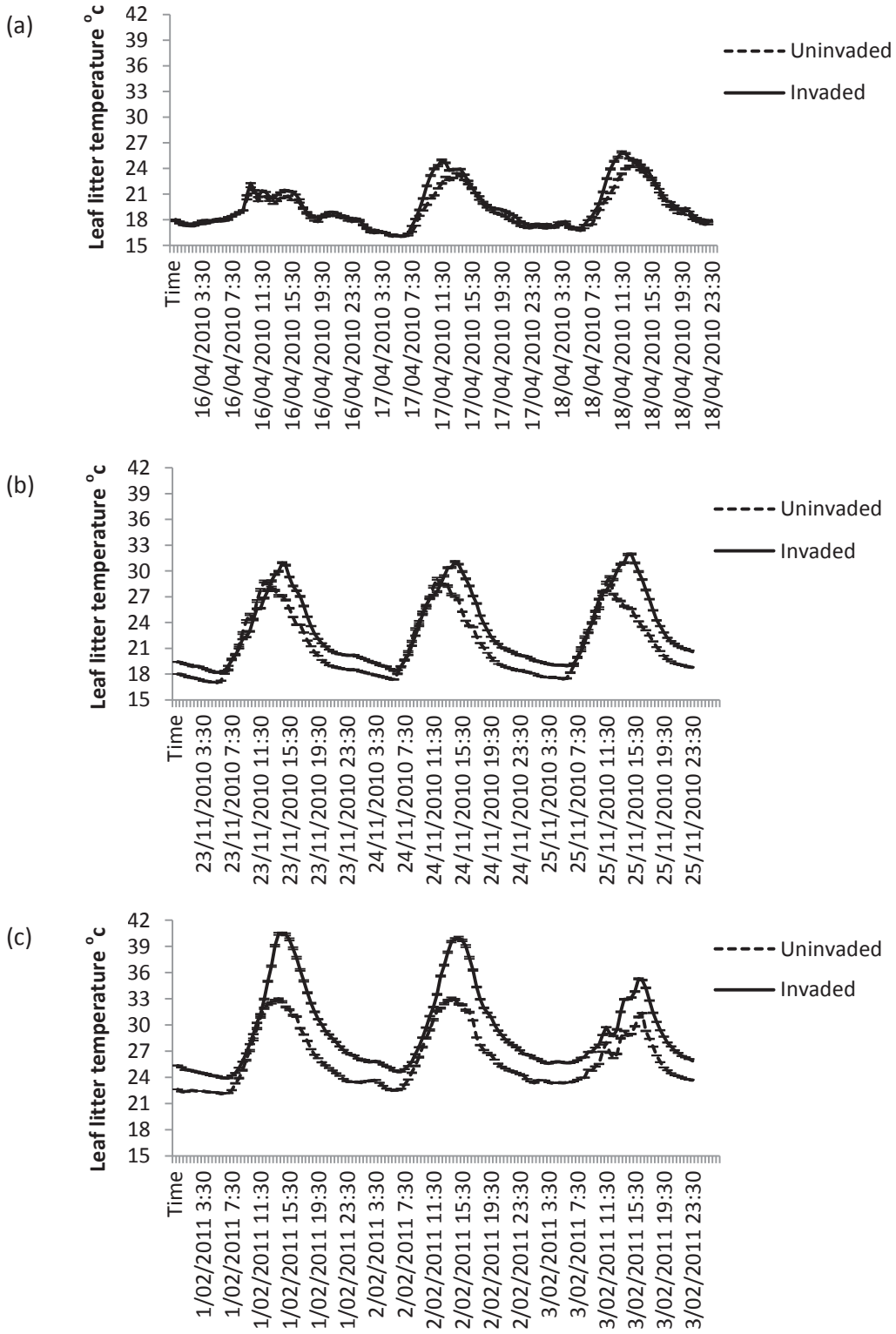

Fig. 5.12. Mean leaf-litter temperatures (± 95% CI) compared between coastal heathland sites invaded by *Chrysanthemoides monilifera* ssp. *rotundata* and uninvaded sites in (a) autumn 2010, (b) spring 2010, (c) summer 2011.

Table 5.4. Results of GLMMs for average leaf-litter temperature during reptile sampling hours (0900-1100 and 1500-1700) in relation to invasion of coastal heathland by *Chrysanthemoides monilifera* ssp. *rotundata*. Significant *P* values are in bold. Condition = invaded or uninvaded, 'Site' is nested within 'Condition'; [1] = $F_{1,30}$, [2] = $F_{1,25}$, [3] = $F_{1,24}$ "-" = non-significant interaction removed from the model as its inclusion led to over-parameterisation of the model.

Season	Condition		Site(condition)	
	F	*P*	*Z*	*P*
Autumn	2.01[1]	0.17	-	-
Spring	7.84[2]	**0.01**	0.80	0.42
Summer	1.92[3]	0.18	0.88	0.38

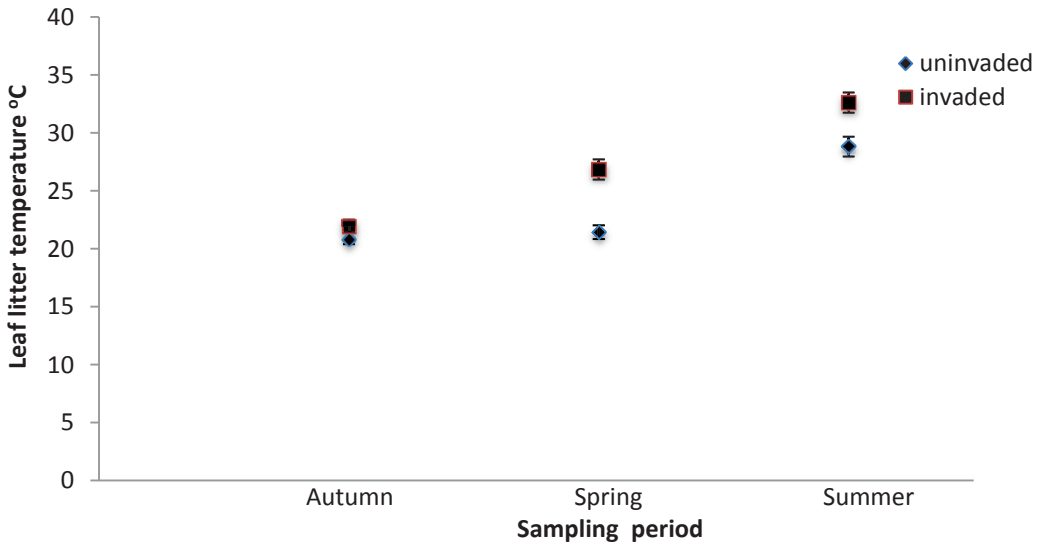

Fig. 5.13. Mean leaf-litter temperatures (± SE) during reptile sampling hours (0900-1100 and 1500-1700) compared between coastal heathland sites invaded by *Chrysanthemoides monilifera* ssp. *rotundata* and uninvaded sites.

maximum reptile activity. In contrast, Bitou Bush did not significantly alter amounts of radiant energy reaching the ground. Leaf-litter temperatures were generally warmer in invaded sites, particularly during afternoon and evening periods, suggesting that Bitou Bush leaf-litter was effective in retaining heat absorbed during the day. This may have important implications for the suitability of invaded habitats for nocturnal reptiles. This should be investigated formally by use of nocturnal surveys, trapping and movement studies to specifically target nocturnal species and investigate their use of invaded and uninvaded habitats.

My results contrast with those of Lindsay & French (2004b) who found differences in habitat structure between Bitou Bush and native coastal vegetation. Bitou Bush was associated with cooler and darker leaf-litter conditions and increases in soil moisture. An important distinction between their study and my investigation is the extent of Bitou Bush cover. Bitou Bush averaged approximately 40% cover at invaded sites in my investigation (Fig. 5.9) whereas the minimum cover of Bitou Bush reported by Lindsay and French (2004b) was 70%. For the purposes of my investigation it was important to ensure that exotic plant coverage was similar between the Lantana and Bitou studies. It is possible that Bitou Bush may exert impacts on reptiles when present in greater density/coverage than was the case in my investigation. A prediction of my Chapter 2 framework is that impacts of exotic plants on reptiles will increase with stand size and coverage area. Exotic plants that modify habitat less strongly will require greater coverage area to exert impacts on reptiles than those that modify habitat more strongly. Thus the differences in Bitou Bush impacts on habitat reported between the two studies are in accord with this prediction. It is also possible that Bitou Bush may be exerting subtle impacts on habitat structure as indicated by a near-significant difference ($P = 0.07$) in understory percentage cover between invaded and uninvaded sites in the Bitou study (Table 5.3). In accordance with the predictions of the framework presented in Chapter 2, any such subtle impact is clearly weaker than the strong impact of Lantana on understorey percentage cover in dry sclerophyll forest ($P = 0.001$) (Table 5.1).

Neither Lantana nor Bitou Bush significantly altered the availability of woody debris on the ground, leaf-litter depth or the amount of bare ground present. These results provide evidence that the differing effects of Lantana and Bitou Bush on the availability of light and shade were driving the different impacts of these exotic plants on reptile abundance. Lantana invasion of dry sclerophyll forest was associated with significantly reduced reptile abundance, particularly of the small-bodied skink *Lampropholis delicata*, whereas Bitou Bush invasion of coastal heathland was not. Changes to the availability and suitability of basking sites and shaded areas have major implications for the suitability of habitats for reptiles. For instance, thermal conditions and shading directly influence habitat preferences of the scincid lizards *Carlia vivax* and *Lygisaurus foliorum* in subtropical areas of northern Australia (Singh *et al*., 2002).

In addition to affecting reptile thermoregulation, overshadowing of habitat by Lantana may also have impacts on reptile reproduction, particularly for oviparous species. Shading of *Crocodylus niloticus* nesting sites in South Africa by the exotic plant *Chromoleana odorata* reduces soil temperatures compared with unshaded nesting sites, potentially inhibiting embryonic development or biasing sex ratios of offspring (Leslie & Spotila, 2001). A number of the reptile species recorded in the Lantana study are oviparous. In particular, *L. delicata* is oviparous and often employs communal nesting (Greer, 1989; Wilson and Swan 2010). Nests may include the output of many females with records of over a hundred eggs in a single nest (Greer, 1989). Thus, overshadowing of potential nesting sites could have severe impacts on reproductive success. Further investigations are required to determine whether Lantana influences nest site selection and reproductive success of oviparous species.

The herbicide treatment of two invaded Bitou Bush sites reduced the level of replication available for determining amounts of solar radiation reaching the ground in the Bitou study. This might raise questions that differences between the impacts of Lantana and Bitou Bush on insolation detected in this study were an artefact of this difference in survey effort. However, re-analysis of insolation data for the Lantana study with two randomly selected Lantana invaded sites omitted (i.e. equivalent replication to the Bitou study) did not alter results. Mean direct photosynthetically

active radiation reaching the ground remained significantly lower in Lantana invaded vegetation (Wald $\chi^2_1 = 5.38$, $P = 0.02$). It is also important to note that coastal heath sites received higher levels of solar radiation than dry sclerophyll forest sites irrespective of whether Bitou Bush was present (Figs. 5.6, 5.11), reflecting differences in the structure of coastal heath and dry sclerophyll vegetation communities. Thus any impact of Bitou Bush on availability of solar radiation in coastal heath habitats is likely to be less critical than the impact of Lantana in dry sclerophyll.

It is possible that avoidance of exotic leaf-litter may also be contributing to reduced abundance of reptiles in dry sclerophyll forest invaded by Lantana. The scincid lizards *Carlia munda* and *Carlia pectoralis* avoid leaf-litter of the exotic vine *Cryptostegia grandiflora* when allowed to choose between native and exotic litter (Valentine *et al*., 2007). The same investigation noted that rubber vine leaves were a different shape than the elongate native leaf-litter, providing less suitable cover with potentially decreased camouflage. Further investigations of reptile habitat preferences, including experiments to manipulate the composition of leaf litter are required to investigate whether reptiles actively avoid Lantana leaf-litter.

Chapter 6: Impacts of Lantana (*Lantana camara*) and Bitou Bush (*Chrysanthemoides monilifera* ssp. *rotundata*) on the availability of invertebrate prey for reptiles

6.1 Introduction

A range of invertebrate taxa feature in the diets of many reptile species (Vitt & Pianka, 2007). A prediction of my framework (Chapter 2) is that exotic plants can exert indirect impacts on reptiles by altering the availability of invertebrate prey. Indeed, there is a growing body of research demonstrating that the incursion of exotic plants into native vegetation causes significant alterations to species richness, composition and abundance of invertebrates (Slobodchikoff & Doyen, 1977; Griffin *et al*., 1989; Herrera & Dudley, 2003; Greenwood *at al.*, 2004; Ernst & Cappuccino, 2005; Robson *et al.*, 2009). Impacts of exotic plants on invertebrate assemblages are linked to exotic plant traits which modify vegetation structure (Slobodchikoff & Doyen, 1977; Herrera & Dudley, 2003; Ernst & Cappuccino, 2005). Thus, the extent to which exotic plants alter the availability of invertebrate prey will likely vary depending on exotic plant traits. The impacts of exotic plant invasion on invertebrates may also act in concert with other direct impacts of exotic plants such as alteration of vegetation structure for reptiles (see Chapter 5).

In Chapter 3, I presented the results of field investigations of the impacts of Lantana (*Lantana camara*) and Bitou Bush (*Chrysanthemoides monilifera* ssp. *rotundata*). I demonstrated that Lantana and Bitou Bush differ in their impacts on reptile abundance. While Lantana invasion of dry sclerophyll forest was associated with significantly reduced reptile abundance, invasion of coastal heathland by Bitou Bush was not. I further demonstrated that, as predicted, the impacts of Lantana were exerted most strongly on smaller-bodied reptile species. In this chapter, I examine the impacts of Lantana and Bitou Bush on the availability of invertebrate prey to determine whether differences between Lantana and Bitou Bush in their impacts on invertebrates underpin their differential invasive impacts on reptile assemblages.

Given that Lantana invasion was linked to a decline in the abundance of small-bodied reptile species, I predict significant negative impacts of Lantana invasion on

leaf-litter invertebrate abundance, richness and consequently composition, in invaded compared with uninvaded sites, if shifts in prey availability underlie observed changes in the reptile assemblage inhabiting dry sclerophyll forest. While I make no *a priori* predictions as to which particular invertebrate taxa are most likely to either decline or dominate in invaded habitats, it is likely that smaller-bodied invertebrate taxa will be the ones to decline given the gape size limitations of diet selection of small-bodied reptile species (Brown, 1989; Greer, 1989). Should I observe no significant impacts of Lantana on invertebrates, then changes to reptile abundance are attributable to other impacts brought about by Lantana invasion such as habitat alteration (see Chapter 5).

Considering that there were no significant impacts of Bitou Bush invasion on reptile abundance, species richness or composition, I predict no significant impacts of Bitou Bush invasion on invertebrate assemblages, if shifts in prey availability lead to changes in the reptile assemblage inhabiting coastal heathland. Any significant negative impacts on invertebrates would indicate that reptiles are displaying dietary opportunism and adapting to changes in invertebrate assemblages brought about by Bitou Bush invasion. Should I observe any positive impacts on invertebrates (e.g. increases in total invertebrate abundance), then factors linked to vegetation structure (see Chapter 5) are precluding reptiles from taking advantage of increased prey abundance and richness.

6.2 Methods

6.2.1 Site descriptions and experimental design

The impacts of Lantana (Lantana study) and Bitou Bush (Bitou study) on leaf-litter invertebrates were studied at the same sites used to investigate impacts of these exotic plant species on reptiles (see Chapter 3 for location details and descriptions of study sites, section 3.2.1).

6.2.2 Invertebrate sampling and identification

For both the Lantana and Bitou studies, invertebrate sampling was conducted concurrently with the reptile sampling described in Chapter 3 in March/April 2010

(autumn), November 2010 (spring) and February 2011 (summer). Invertebrates were sampled using unbaited pitfall traps placed along the same permanent transects used for reptile surveys; i.e. a transect was located 2.5 m from the vegetation edge with further transects at 15 m intervals. Four pitfall traps were used per transect with the first trap placed 2.5 m from the start of the transect and the remaining traps at 15 m intervals along the transect. Four transects were used in large plots (Fig. 6.1) and two in small plots (Fig. 6.2). Each trap comprised two 450 ml plastic drinking cups (9 cm in diameter, 11.5 cm deep). The cups were placed one inside the other and buried with the lip of the top cup flush with the ground (Fig. 6.3a). To eliminate any 'digging-in' effects, traps were installed and remained closed for at least two weeks prior to the first sampling period in each study. Traps remained *in situ* between sampling periods and only the top cup was removed when emptying traps (Majer, 1978; Digweed *et al.*, 1995; Ernst & Cappuccino, 2005). A preservative solution of 1:1 ethylene glycol (Prestone™ antifreeze) and water was placed in each trap to a depth of approximately 3 cm. To prevent vertebrates from being captured in traps during sampling periods, traps were covered with close fitting 11 cm x 11 cm wooden lids which were anchored to the ground using four nails in the corners of the cover (Ausden & Drake, 2006). Traps were opened by raising the covers approximately 10 mm above the surface of the trap (Fig. 6.3b) during sampling periods. Traps were kept closed between sampling periods by lowering the covers flush to the ground.

Traps were left open for 5 days during each sampling period with all sites within a study sampled concurrently. At the conclusion of each sampling period the contents of each trap were emptied into separate 50 ml sample jars labelled with site, transect and trap number. Invertebrates were then transported to the laboratory and stored in 70% ethanol for later sorting. In the Lantana study, one control site (LC2 Belmont) and one invaded site (LI3 Little Pelican Reserve) could not be sampled in spring 2010. Access to these sites during the spring survey period was prevented by localised flooding. In the Bitou study, two invaded sites (BI1 Kurnell and BI4 La Perouse) were subjected to herbicide treatment of Bitou Bush by the NSW National Parks and Wildlife Service soon after the completion of the autumn 2010 survey. These

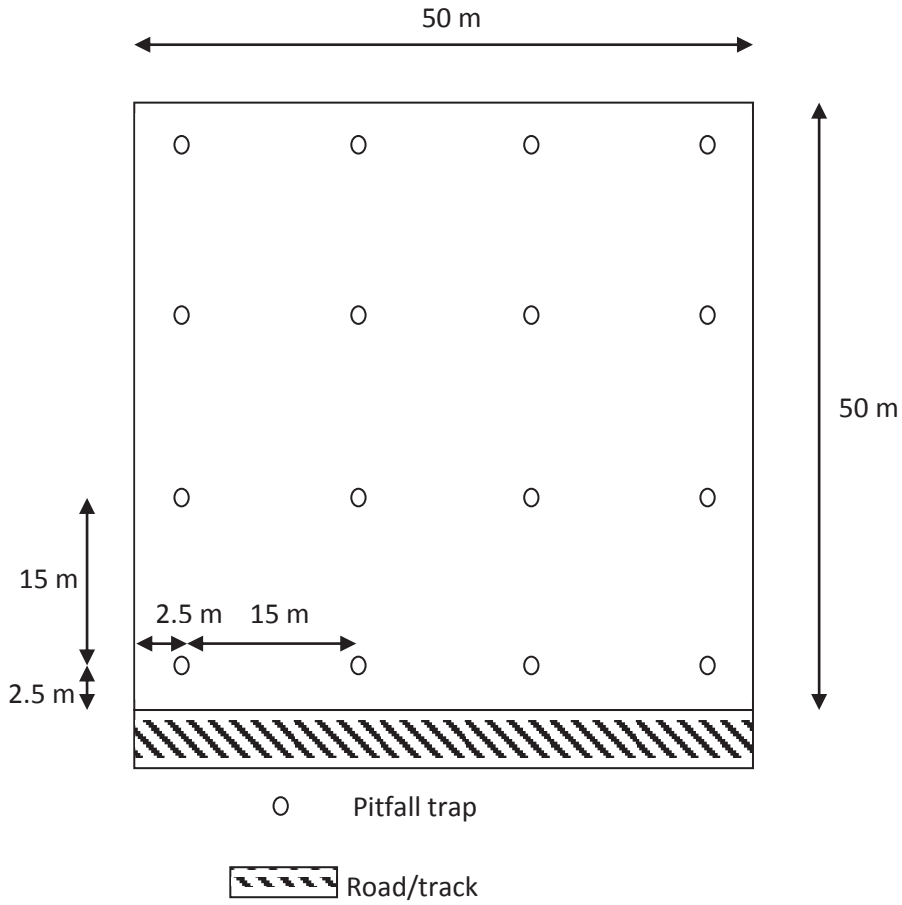

Fig. 6.1. Arrangement of invertebrate pitfall traps in large (50 m x 50 m) study plots.

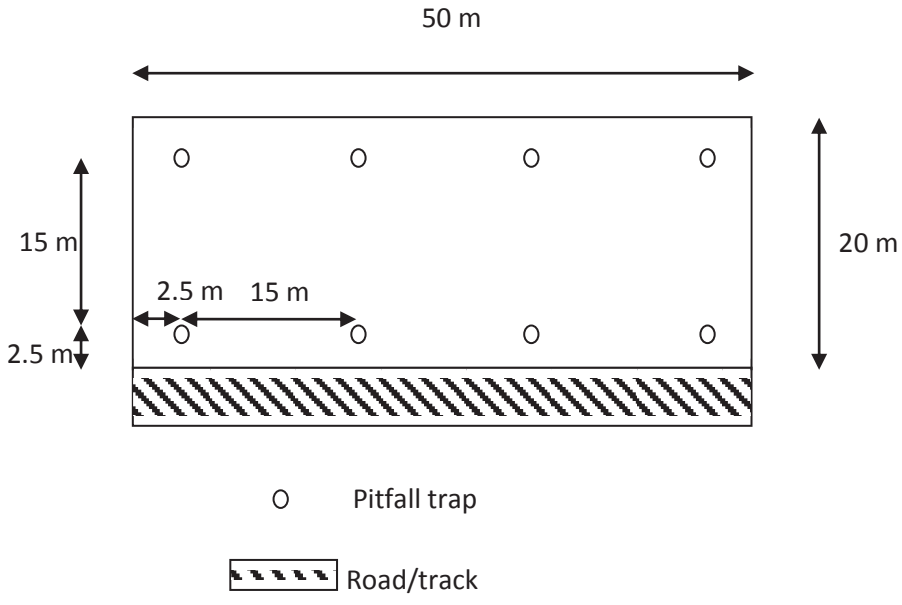

Fig. 6.2. Arrangement of invertebrate pitfall traps in small (50 m x 20 m) study plots.

(a) (b)

Fig. 6.3. Invertebrate pitfall trap (a) and wooden cover to exclude vertebrates (b).

sites were not used in comparisons between invaded and uninvaded vegetation in the spring 2010 and summer 2011 surveys for the purposes of the predictions of this chapter.

Invertebrates were sorted to taxonomic order under a dissecting microscope using the taxonomic keys of Harvey & Yen (1989) and further sorted to morphospecies based on distinctive morphological features. The morphospecies method provides a rapid, accurate and effective surrogate for species in environmental monitoring and biodiversity studies (Oliver & Beattie, 1993, 1996a, 1996b; Lindsay & French, 2006b). No larvae were identified other than those from the order Lepidoptera. This did not have a major impact on the numbers of invertebrates recorded as few larvae belonging to orders other than Lepidoptera were captured. Voucher specimens of each morphospecies were retained and preserved in 50 ml sample jars containing 70% ethanol. Total invertebrate abundance, abundance of each morphospecies and morphospecies richness were determined for each transect and averaged to give (per transect) site values.

6.2.3 Statistical analyses

Data for total invertebrate abundance and morphospecies richness were analysed using separate general linear models (GLMs) in SPSS v.20. 'Condition' (invaded or uninvaded) and 'Time' (autumn 2010, spring 2010, summer 2011) were fixed factors

and an interaction term for Condition x Time was included in the models. Data for total invertebrate abundance and morphospecies richness were checked for normality using Kolmogorov-Smirnov tests and for homogeneity of variances using Levene's test. Data for total invertebrate abundance and morphospecies richness in the Lantana study were ln(x) transformed to improve normality and homogeneity of variances. Data for total invertebrate abundance and morphospecies richness in the Bitou study satisfied GLM assumptions and were not transformed. All graphs depict untransformed data to assist interpretation. Tukey's HSD post-hoc tests were performed, where necessary, to explore significant differences in invertebrate abundance and morphospecies richness among the three sampling times (autumn, spring and summer).

Invertebrate assemblage compositions were analysed using PRIMER v.5.2.9. Morphospecies abundance data were square root transformed and non-metric multidimensional scaling (nMDS) was used to explore differences in the composition of invertebrate assemblages among habitat conditions after calculation of Bray-Curtis similarity indices. One-way analysis of similarity (ANOSIM) was used to test dissimilarities in invertebrate assemblages. Data for each sampling season were analysed separately due to the identification of significant Time effects on invertebrate abundance and morphospecies richness in the Lantana study.

6.3 Results

6.3.1 Lantana study

There was no significant effect of Condition on invertebrate abundance (Table 6.1; Fig. 6.4). There was a significant effect of Time on invertebrate abundance (Table 6.1; Fig 6.4). Abundance was significantly higher in spring than in autumn (Tukey's HSD: $P < 0.001$) or summer (Tukey's HSD: $P < 0.001$). There was no significant difference in invertebrate abundance between autumn and summer (Tukey's HSD: $P = 1.000$). This seasonal trend was apparent in both invaded and uninvaded vegetation with no significant interaction between Condition and Time detected (Table 6.1).

There was no significant effect of Condition on invertebrate morphospecies richness (Table 6.1; Fig. 6.5). There was a significant effect of Time (Table 6.1; Fig 6.4). Morphospecies richness was significantly higher in spring than in autumn (Tukey's HSD: $P < 0.001$) and summer (Tukey's HSD: $P < 0.001$) and significantly higher in summer than in autumn (Tukey's HSD: $P = 0.013$). The interaction between Condition and Time was not significant (Table 6.1).

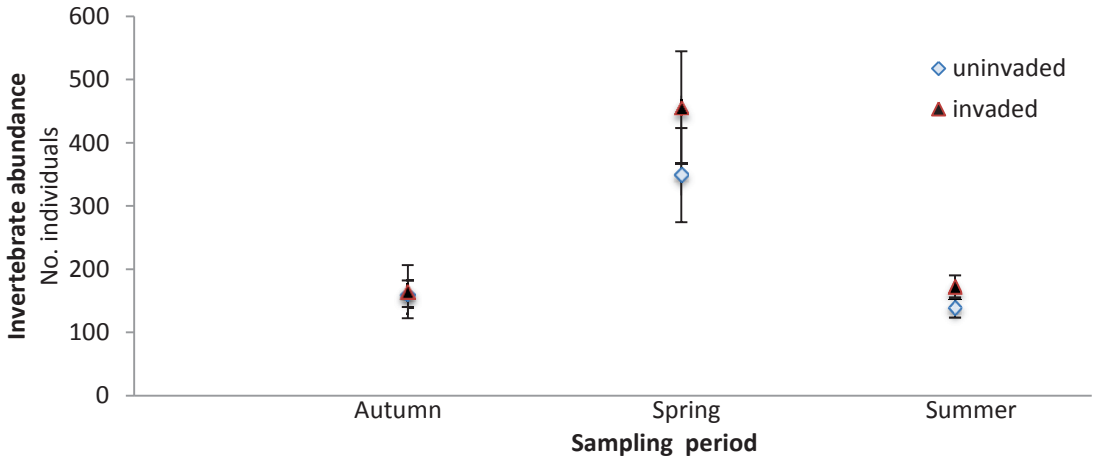

Fig. 6.4. Mean abundance (± SE) of invertebrates compared between sites of dry sclerophyll forest invaded by *Lantana camara* and uninvaded sites.

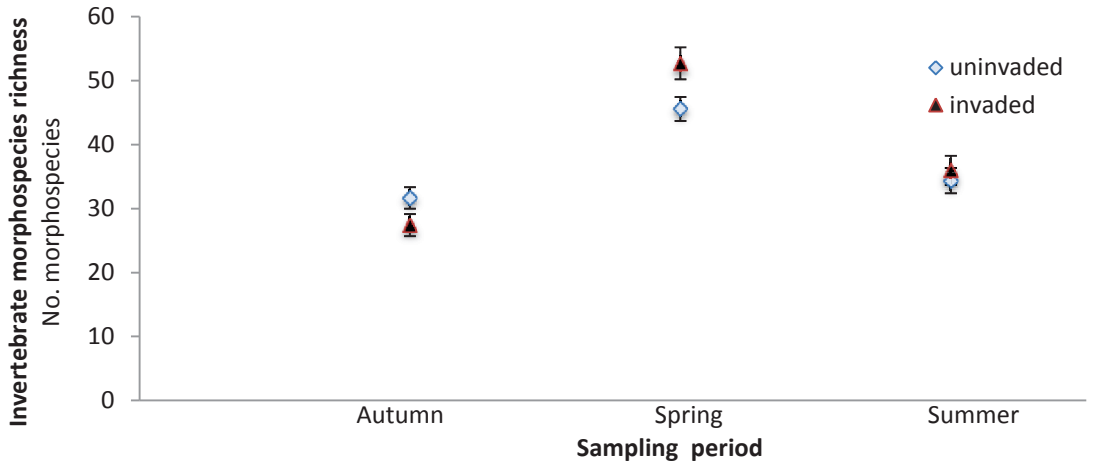

Fig 6.5. Mean invertebrate morphospecies richness (± SE) compared between sites of dry sclerophyll forest invaded by *Lantana camara* and uninvaded sites

Table 6.1. GLM results for invertebrate abundance and morphospecies richness in relation to invasion of dry sclerophyll forest by *Lantana camara*. Significant *P* values are in bold. 'Condition' = invaded or uninvaded, 'Time' = autumn, spring or summer.

	Condition		Time		Condition*Time	
	$F_{1,22}$	*P*	$F_{2,22}$	*P*	$F_{2,22}$	*P*
Abundance	1.06	0.31	16.91	**< 0.001**	0.53	0.60
Species richness	0.08	0.78	37.53	**< 0.001**	3.16	0.06

The composition of leaf-litter invertebrate assemblages was similar between invaded and uninvaded sites in each of the three sampling periods. ANOSIM results revealed non-significant differences between the two habitat conditions (Table 6.2). This was reflected in nMDS plots for each season which showed only indistinct clustering of sites within each habitat condition. Furthermore, nMDS plot distances between sites within each habitat condition were similar to distances between sites of different habitat conditions (Fig. 6.6).

Table 6.2. ANOSIM results comparing invertebrate assemblages between dry sclerophyll sites invaded by *Lantana camara* and uninvaded sites in autumn 2010, spring 2010 and summer 2011.

Sampling period	Global R	*P*
Autumn	0.224	0.08
Spring	-0.125	0.80
Summer	-0.032	0.57

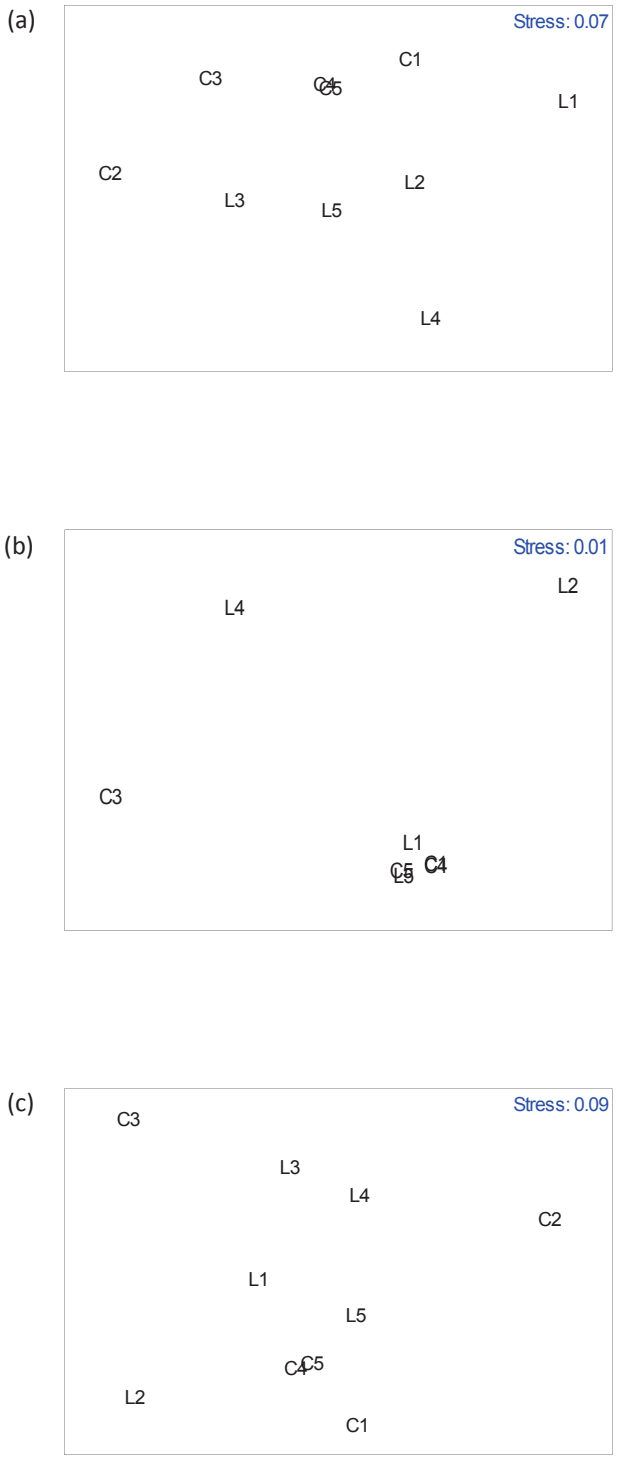

Fig. 6.6. Non-metric multidimensional scaling (nMDS) plots comparing the composition of leaf litter invertebrate assemblages between dry sclerophyll forest sites invaded by *Lantana camara* (L1-L5) and uninvaded forest sites (C1-C5) in (a) autumn 2010, (b) spring 2010 and (c) summer 2011.

6.3.2 Bitou study

Total invertebrate abundance was significantly higher in invaded sites than in uninvaded sites (Table 6.3; Fig. 6.7). This was the case in each sampling period with no significant effect of Time detected, nor was there was any significant interaction between Condition and Time. There was no significant effect of Condition on invertebrate morphospecies richness (Table 6.3; Fig. 6.8). No significant effects of Time or the interaction between Condition and Time were detected.

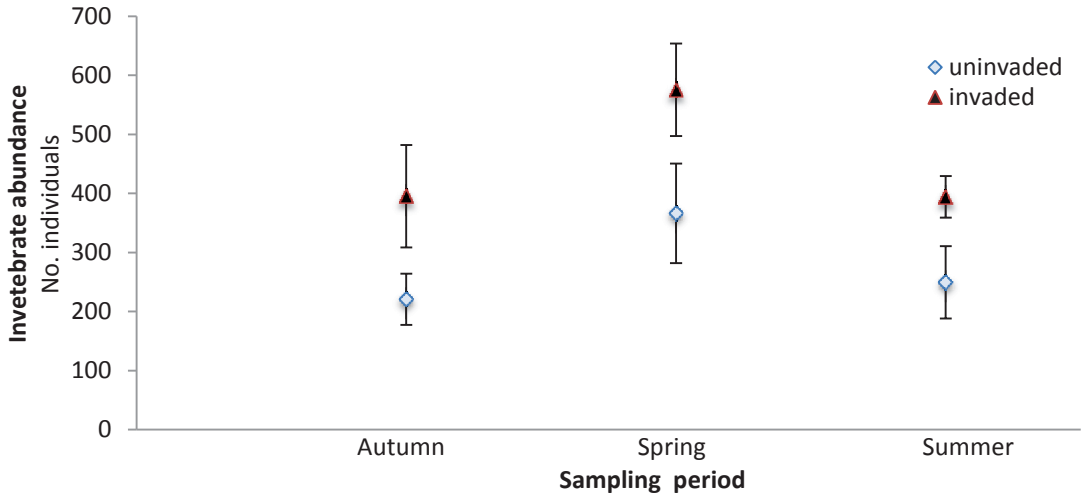

Fig. 6.7. Mean abundance (± SE) of invertebrates compared between sites of coastal heathland invaded by *Chrysanthemoides monilifera* ssp. *rotundata* and uninvaded sites.

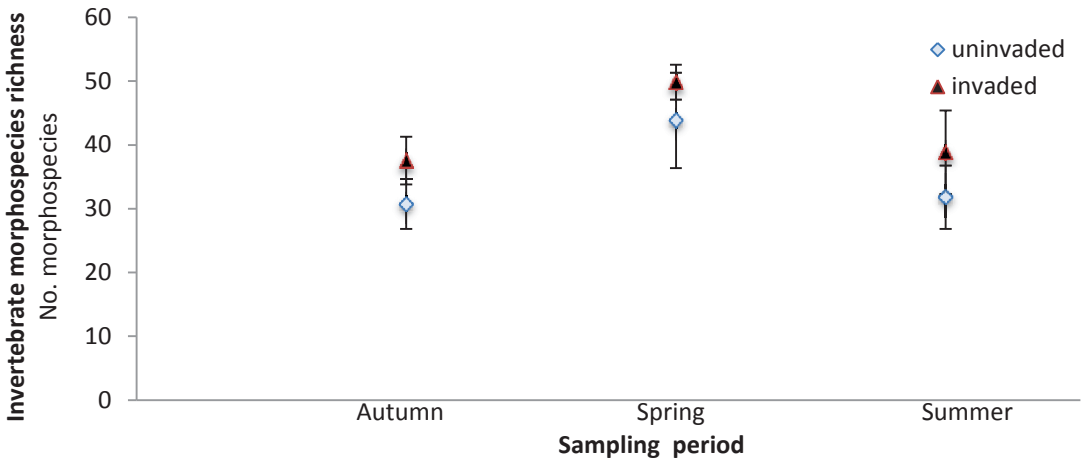

Fig. 6.8. Mean invertebrate morphospecies richness (± SE) compared between sites of coastal heathland invaded by *Chrysanthemoides monilifera* ssp. *rotundata* and uninvaded sites.

Table 6.3. GLM results for invertebrate abundance and morphospecies richness in relation to invasion of coastal heathland by *Chrysanthemoides monilifera* ssp. *rotundata*. Significant *P* values are in bold. 'Condition' = invaded or uninvaded, 'Time' = autumn, spring or summer.

	Condition		Time		Condition*Time	
	$F_{1,20}$	*P*	$F_{2,20}$	*P*	$F_{2,20}$	*P*
Abundance	8.49	**0.01**	2.90	0.08	0.09	0.92
Species richness	2.15	0.16	3.15	0.07	0.01	0.99

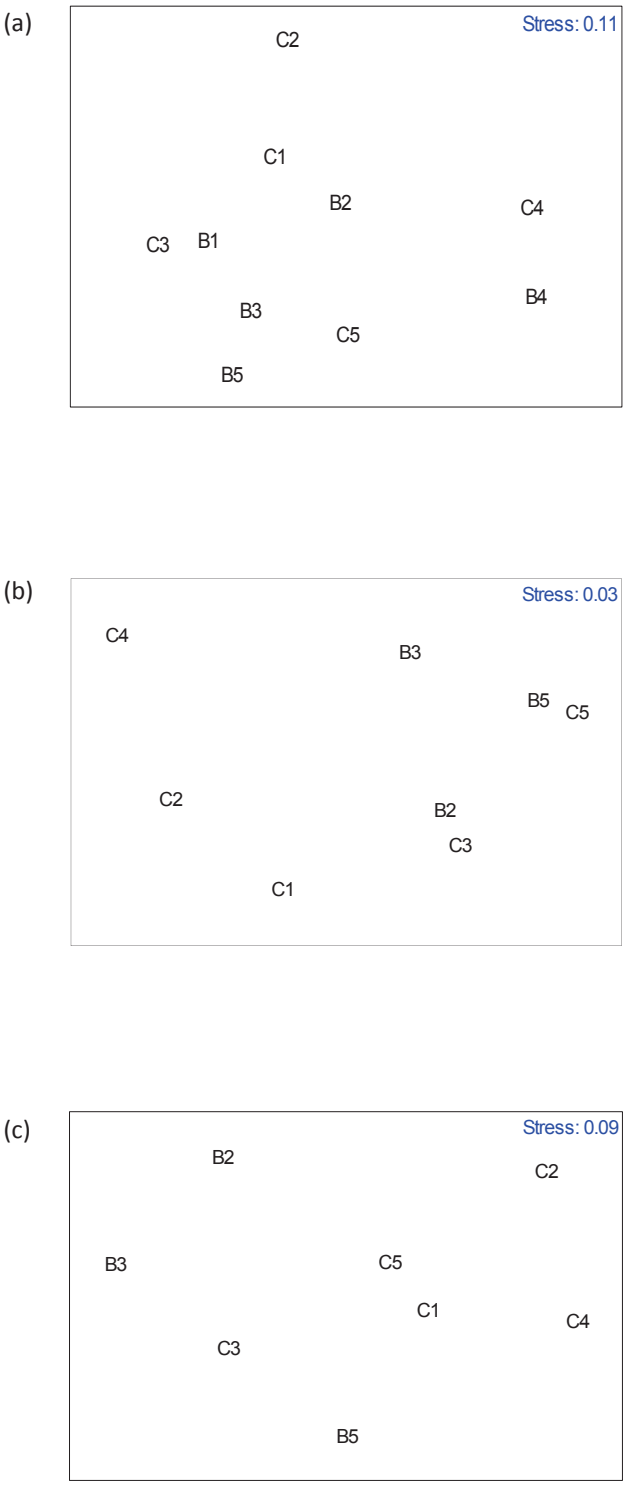

Fig. 6.9. Non-metric multidimensional scaling (nMDS) plots comparing the composition of leaf litter invertebrate assemblages between coastal heathland sites invaded by *Chrysanthemoides monilifera* ssp. *rotundata* (B1-B5) and uninvaded sites (C1-C5) in (a) autumn 2010, (b) spring 2010 and (c) summer 2011.

Table 6.4. ANOSIM results comparing invertebrate assemblages between coastal heathland sites invaded by *Chrysanthemoides monilifera* ssp. *rotundata* and uninvaded sites in autumn 2010, spring 2010 and summer 2011.

Sampling period	Global R	*P*
Autumn	-0.016	0.54
Spring	-0.087	0.64
Summer	0.344	0.07

The composition of leaf-litter invertebrate assemblages was similar between invaded and uninvaded sites in each of the three sampling periods. ANOSIM results revealed non-significant differences between the two habitat conditions (Table 6.4). This was reflected in nMDS plots for each season which showed only indistinct clustering of sites within each habitat condition. The nMDS plot distances between sites within each habitat condition were also similar to distances between sites of different habitat conditions (Fig. 6.9).

6.4 Discussion

Lantana and Bitou Bush differed in their impacts on leaf-litter invertebrates. While Lantana did not alter the abundance or morphospecies richness of invertebrate assemblages, Bitou Bush was associated with significantly higher abundance of invertebrates (but no difference in species richness) when compared with uninvaded sites. Importantly, neither species appeared to reduce the availability of invertebrate prey for reptiles. The lower abundance of reptiles, and in particular, the reduced abundance of the small-bodied *Lampropholis delicata* in dry sclerophyll forest invaded by Lantana was thus not associated with any significant changes to the leaf-litter invertebrate assemblage. Interestingly, the higher abundance of invertebrates in costal heathland invaded by Bitou Bush did not correspond with any increase in reptile abundance. Together, these results suggest that prey availability is not linked to the abundance of reptiles in either the Lantana or the Bitou studies. Furthermore, despite strong seasonal effects on abundance and morphospecies richness of invertebrates in

the Lantana study, no significant seasonal effect on reptile abundance was identified (see Chapter 3). This provides further evidence that fluctuations in prey availability were not strongly linked to the abundance of reptiles. It is interesting to note a near-significant effect of time on invertebrate abundance and species richness in the Bitou study (Table 6.3), with both recording higher values in spring than in autumn or summer (Fig. 6.7; Fig. 6.8). This is similar to the strong seasonal trends identified in the Lantana study (Table 6.1; Fig. 6.4; Fig. 6.5). These results suggest some degree of similarity in the responses to environmental conditions of invertebrate communities in the two habitat types, with seasonal influences exerting stronger effects than the presence or absence of exotic vegetation. It is also interesting to note that, similarly to the Lantana study, these seasonal variations in invertebrate abundance and species richness were not linked to any significant seasonal effect on reptile abundance.

It is possible that Lantana and Bitou Bush exert influences on prey availability beyond those discernible at the broad level of morphospecies used in this investigation. A near-significant interaction between Condition and Time for species richness in the Lantana study (Table 6.1) and near-significant ANOSIM results comparing invertebrate assemblages between invaded and uninvaded sites for the Lantana study in autumn (Table 6.2) and the Bitou study in summer (Table 6.4) may indicate subtle differences in the responses of invertebrates to seasonal weather variations between invaded and uninvaded habitats. Further research including studies undertaken over several years and identification of invertebrates to higher levels of taxonomic resolution than morphospecies are required to explore this further.

Total abundance of invertebrates may not directly reflect the abundance of prey for dietary specialists (Greer, 2001). For example, three sympatric skink species of the genus *Carlia* have been found to selectively consume prey types and prey sizes that were not abundant in their habitat (Manicom & Schwarzkopf, 2011). Selectivity may also occur at the intraspecific level of prey items. For example, the small scincid lizard *Cryptoblepharus virgatus* has been observed to selectively prey upon alates of small ants while actively avoiding worker ants, possibly due to higher fat content of

alates (Greer, 2001). I don't believe this to be the case, however, in my study. In general, the majority of small reptiles are generalist invertebrate predators with flexible foraging behaviours (Greer, 1989; Brown, 1991). This includes species encountered in this investigation such as *Lampropholis delicata*, *L. guichenoti* (Crome, 1981; Greer, 1989; Lunney *et al.*, 1989; Brown, 1991), *Ctenotus taeniolatus* (Taylor, 1986) and *Amphibolurus muricatus* (Greer, 1989). Furthermore, both *L. delicata* and *L. guichenoti* have been shown to alter diet in response to events such as drought and fire that are likely to alter arthropod abundance (Lunney *et al.*, 1989), which suggests a high degree of dietary flexibility.

Differences in body sizes of invertebrates between invaded and uninvaded habitats may also be important. The size of prey items taken by reptiles is related to head and gape size with larger prey items being taken by larger reptile species (Brown, 1989). Prey type may also be influenced by body size, gape size and jaw strength with larger lizards consuming a greater proportion of hard-bodied invertebrates such as Coleoptera, compared with smaller lizards (Brown, 1989). Nevertheless, the lack of any significant effect of either Lantana or Bitou Bush on invertebrate assemblage composition suggests that there were no effects on the availability of preferentially selected prey species or prey size. Further research, however, including analysis of reptile stomach contents is required to confirm that diet does not differ between invaded and uninvaded sites.

The findings for the invertebrate assemblages in my study are supported in part, but not completely, by the results of previous studies. Barkley (2010) found that small-scale infestations of Lantana had no impact on the abundance or diversity of leaf-litter invertebrates in the Lower Hunter region, the broad region in which the Lantana study of the present investigation was conducted. However, Lindsay & French (2006) found that Bitou Bush invasion in areas of the NSW coast did not affect the total abundance of leaf-litter invertebrates. They did find that some taxa were higher in invaded areas, taxa such as millipedes, amphipods and isopods, but this was matched by declines in other taxa such as mites, thrips and spiders. An important distinction between their study and my investigation is the extent of Bitou Bush cover. Bitou Bush

averaged approximately 40% cover at invaded sites in my investigation whereas the minimum cover of Bitou Bush reported by Lindsay and French (2004b) was 70%. For the purposes of my investigation it was important to ensure that exotic plant coverage was similar between the Lantana and Bitou studies. It is possible that impacts of Bitou Bush on invertebrates may vary with density/coverage.

Chapter 7: A comparison of short-term marking methods for small frogs using a model species, the striped marsh frog (*Limnodynastes peronii*).

7.1 Introduction

Marking individuals for identification and tracking of movement is critical in population studies as a means of avoiding pseudoreplication and biased estimates of abundance (Corn, 1994; Mellor *et al*., 2004). For amphibians, commonly used long-term (months to years) marking techniques include toe clipping, branding and tattooing (Donnelly *et al*., 1994; Halliday, 2006; Ferner, 2007). Some studies have employed fluorescent dyes for marking through the use of heat (Ireland, 1973), compressed air (Nishikawa and Service, 1988; Brown, 1997), or abrasion (Ireland, 1991) to allow dyes to penetrate. Other studies have used acrylic polymers, visible implant elastomers (VIE), visible implant alphanumeric (VIA) tags or passive integrated transponder (PIT) tags for marking, all of which involve subcutaneous injection (Woolley, 1973; Davis and Ovaska, 2001; Ferner, 2007; Heard *et al*., 2008). Visible implant elastomers have also been combined with toe clipping (VIE-C) to improve the reliability of identification (Hoffman *et al*., 2008; Campbell *et al*., 2009).

While all of these long-term marking techniques are valuable for amphibian research in that they can produce marks that last for months or years, one disadvantage is that their invasiveness can lead potentially to an increased risk of infection, pain, injury, reduced locomotor performance, behavioural alterations or mortality in frogs (Clarke, 1972; Golay and Durrer, 1994; Davis and Ovaska, 2001; Schmidt & Schwarzkopf, 2010). Furthermore, techniques requiring the use of compressed air may not be suitable for use on very small or fragile frogs (Nishikawa and Service, 1988; Nishikawa, 1990) while PIT tags may also be unsuitable for some frogs smaller than 40mm SVL (Johnson, 2009). In addition, for studies requiring only short-term marking of frogs (i.e. over one to three days), the costs associated with long-term marking techniques are unwarranted. Thus, there is considerable need to develop minimally-invasive, low injury risk marking methods for small frogs for research where marks need only be retained for short periods. Such research needs

include visual encounter or trapping studies conducted over a period of several days or nights and short-term studies of animal movement and behaviour. Pattern mapping of individual markings (Donnelly *et al*., 1994; Halliday, 2006; Ferner, 2007) offers a minimally-invasive recognition method that has been used successfully in large-scale studies (see Gill, 1978; Davis & Grayson, 2007), but this technique is not suitable for species that lack identifiable individual markings or where temporal shifts in patterning occur (Johnson, 2009). The technique may also be time consuming and difficult to use reliably on large populations (Johnson, 2009).

In this study, I performed a manipulative experiment under laboratory conditions to compare the retention times of three short-term, minimally-invasive skin marking methods for frog identification. The methods were: the application of one of two medical dyes, gentian violet and mercurochrome, used for the treatment of minor injuries and infections in humans and animals, or the application of fluorescent powder, all without skin abrasion, heat or compressed air.

7.2 Methods

7.2.1 Experimental design and marking procedures

For the purposes of this study, I focussed on a model species representative of small frogs, *Limnodynastes peronii* (the striped marsh frog), which has a body size of 46-73mm (Tyler & Knight, 2011). Additionally, adults of the species display average size and life-history traits common to many Australian frog species.

Frogs were obtained from captive bred stock produced by a licensed amphibian breeder and all were transferred to a licensed amphibian keeper at the conclusion of the experiment for ongoing care.

In the laboratory, individual frogs were each housed separately in identical plastic aquaria (length 31 cm, width 18 cm, height 21 cm). The aquaria contained water and land areas; leaf litter, bark and aquatic plants provided retreats and environmental enrichment. Substrate for land areas consisted of moistened coconut husk fibre (Exo-Terra Plantation Soil™, Exo-Terra) which allowed frogs to burrow beneath leaf litter.

The frogs were fed every 2-3 days on live crickets, dusted with vitamin and calcium supplement powder and were maintained in these conditions for 1 week prior to the beginning of the experiment.

Frogs were divided randomly into one control (unmarked) and three treatment groups with five animals in each of the four groups. Frogs in the treatment groups were marked with either 1% weight/volume (w/v) gentian violet, 2% w/v mercurochrome or yellow powdered fluorescent pigment (Glow Paint Industries, Glow in the Dark Pigment, median particle diameter: d50≤6.0±0.5 μm) on 23 December 2009. Control group frogs were handled and weighed but not marked in order to control for the procedural technique. Marks were applied by using a cotton bud to paint a whole foot. No attempt was made to abrade the skin in order to increase penetration of dye or pigment; however, gentle pressure was used to assist in the application of fluorescent pigment. Visibility of marks was checked once daily until all marks had disappeared. Visual assessments of mark presence or absence were conducted with frogs remaining in aquaria. Fluorescent pigment marks were assessed under both ambient light and with a UV light source (Loon UV Mini-Lamp™, Loon Outdoors). All inspections were conducted by the same observer at a distance of approximately 30cm from each frog. Observations were made at the same time each day.

All frogs were observed for 60 minutes following application of marks to check for adverse reactions. Normal, resting behaviour resumed within 10 minutes of the application of marks for all animals. I visually inspected each frog twice daily from 23 December 2009 until 2 January 2010 to check for signs of ill health. Frogs were weighed immediately prior to marking and five days after marking to identify any differences in weight loss or gain between control and treatment groups. Normal, resting behaviour resumed within 10 minutes of the application of marks for all animals. No signs of pain or irritation in response to marking were observed and no signs of ill health were detected at any time over the course of the experiment.

7.2.2 Statistical analyses

Data for mark retention (presence or absence of marks at each inspection) and weight change were analysed using separate one-way ANOVA in SPSS v17. Fisher's least significant difference (LSD) post-hoc tests were used to determine whether there were differences in mark retention times between the experimental groups. This included an analysis of whether retention times differed significantly from the control group. This is important in determining whether marking provides any advantage in identifying individuals (e.g. recaptures) over not marking.

7.3 Results

Retention times of marks applied to frogs differed significantly among the experimental groups ($F_{3,16}$ = 19.93, P < 0.0001) (Fig. 7.1). Mean retention times for each of the three treatment groups differed significantly from the control group (LSD tests: gentian violet P < 0.0001, mercurochrome P < 0.05, fluorescent pigment P < 0.05). Markings using gentian violet were retained for between two and four days (mean ± SE = 2.4 ± 0.4). This was significantly longer than retention times for both mercurochrome (LSD test: P < 0.0001) and fluorescent pigment (LSD test: P < 0.0001). Nevertheless, mercurochrome was retained for at least one day by all frogs (mean ± SE = 1.0 ± 0.0) while fluorescent pigment was either not retained at all or for one day at most (mean ± SE = 0.8 ± 0.2).

All groups of frogs gained weight during the experimental period (Fig. 7.2) with no significant differences among groups in weight change ($F_{3,16}$ = 0.449, P > 0.05).

7.4 Discussion

Gentian violet provided longest lasting marks of the three treatments used. Detectability of gentian violet marks may have been assisted by the fact that gentian violet was observed to contrast more strongly with striped marsh frog colouration than mercurochrome. Further investigation is required to determine if this is an important factor in the choice of marking agents. The short retention times for fluorescent

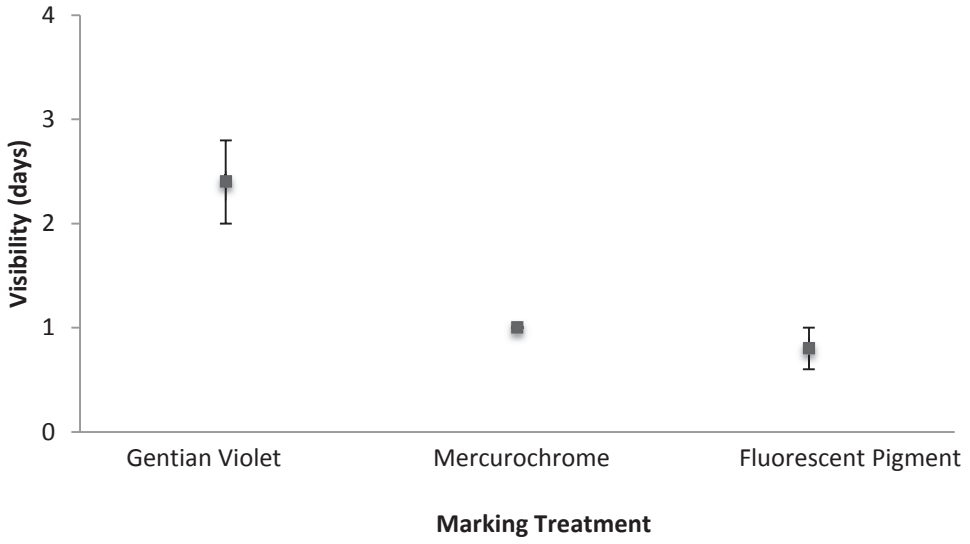

Fig. 7.1. Retention times (days) for marks applied to feet of *Limnodynastes peronii* using gentian violet, mercurochrome and powdered fluorescent pigment.

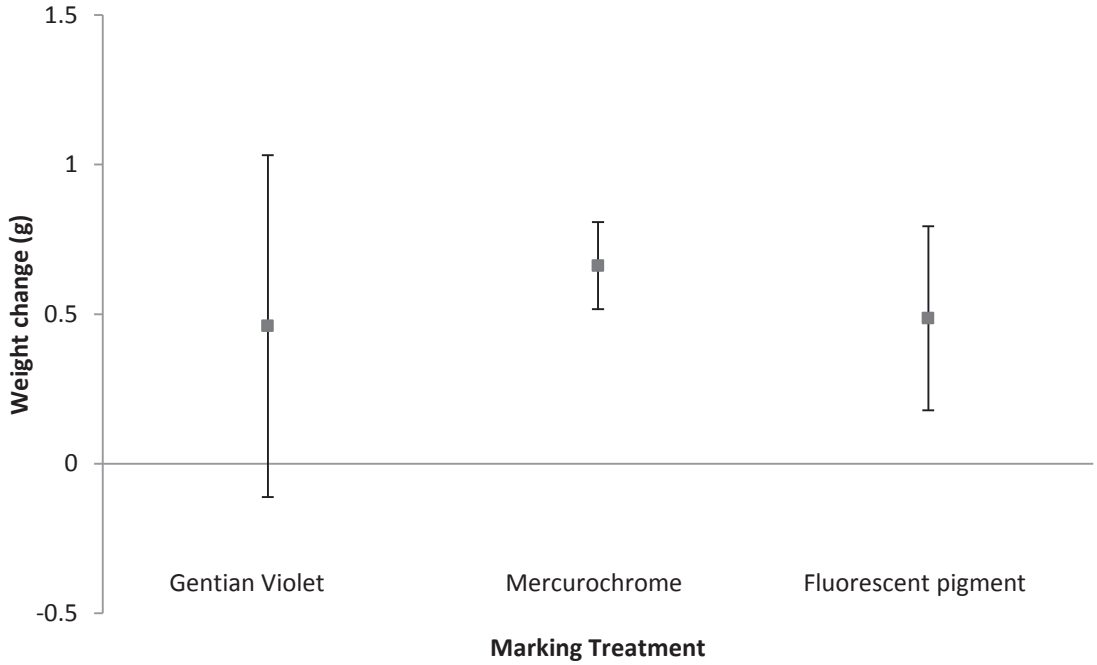

Fig. 7.2. Weight change (day 1 to day 5) of *Limnodynastes peronii* marked with either gentian violet, mercurochrome or powdered fluorescent pigment.

pigment marks suggest that fluorescent pigment may not be reliable for short-term studies where identification is required. However, powdered fluorescent pigment remains a useful tool for tracking amphibian movements as this approach relies on animals shedding pigment to create a trail detectable by ultraviolet light (Windmiller, 1996; Birchfield & Deters, 2005).The fact that all frogs gained weight suggests that none of the marking methods tested here lead to adverse changes in animal condition. This is important because marking methods should have minimal effects on survivorship or behaviour (Mellor *et al*., 2004; Ferner, 2007).

Although my experimental work was based on one model frog species, my findings indicate that skin-staining with gentian violet represents a promising alternative to more invasive techniques for studies where long-term mark retention is not required. To build on this finding, I recommend both further testing with gentian violet on a range of amphibian species to assess the suitability for general amphibian use as well as testing with additional dye types to determine their potential for longer retention times of marks. Further studies should also be conducted to test for longer-term reactions to skin staining.

Chapter 8: General discussion

8.1 Were the objectives of this thesis met?

The principal aim of this thesis was to provide a means of predicting the impacts of exotic plant invasions on reptiles and amphibians and determining management priorities. In Chapter 1 I identified a number of objectives that needed to be met to achieve this goal. These objectives have been met as follows:

1. To identify invasive exotic plant and native reptile and amphibian life-history traits that influence the response of reptiles and amphibians to exotic plant invasion.
In Chapter 2 I drew upon ecological theory to identify growth form, area of coverage and taxonomic distinctiveness from native vegetation as exotic plant traits influencing the likelihood of invasion producing impacts on reptiles and amphibians. I further identified animal body size, lifespan, home range size, habitat specialisation, diet and reproductive strategy as life-history traits determining the sensitivity of reptiles and amphibians to impacts from exotic plant invasions.

2. To develop a framework that describes how these plant and animal life-history traits interact to determine the magnitude and scope of impacts of exotic plant invasions.
The framework presented in Chapter 2 integrates these plant and animal life-history traits into three mechanistic models. These models are based on exotic plant invasion altering: (1) habitat structure; (2) herbivory and predator-prey interactions; and (3) the reproductive success of reptile and amphibian species and assemblages. From these models I derived predictions describing the impacts of exotic plant invasions on reptiles and amphibians. I predicted that exotic plants exhibiting novel growth forms, structural features and large spatial coverage will exert stronger and more rapid influences on reptiles and amphibians via each of these three mechanisms compared with exotic plants that replicate existing growth forms and structural features and have small spatial coverage. I also predicted that these impacts would be exerted most

strongly on reptiles and amphibians with small body size, small home range, dietary specialisation, habitat specialisation, short lifespan and oviparity.

3. To test model predictions against currently available empirical evidence in the literature.

An extensive literature review (Chapter 2) provided evidence to support predictions from all three model mechanisms in relation to reptiles. There was strong evidence that exotic plants exhibiting novel growth forms or structural features exert impacts on reptiles by altering habitat structure and quality, including leaf-litter structure, availability of woody debris and availability of light and shade. The literature also provided evidence to support predictions relating to exotic plant impacts on reptiles via altered predator-prey interactions. Predictions relating to impacts on reproduction in oviparous species were also supported by available evidence. There was also evidence to support the prediction that impacts of exotic plants on reptiles increase with increasing area of exotic plant coverage.

The majority of studies in the literature focused on the impact of individual exotic plant species. These studies provided important information on the impacts of exotic plants that modify habitat structure strongly; however, their single-species focus made it difficult to make comparisons between those species studied and other exotic plant species that exhibit similar growth forms to the native vegetation. Comparison of the impacts of exotic plant species with differing effects on habitat structure was identified as a priority for field research.

Less evidence was available to test model predictions in relation to amphibians, due to the relative paucity of studies investigating the impacts of invasive exotic plants on amphibians. Nevertheless, there was evidence to support predictions that changes to vegetation structure and composition resulting from exotic plant invasion can reduce foraging efficiency in amphibians. There was also evidence to support the prediction that alteration of habitat structure by exotic plants may affect reproductive success of amphibians by altering the suitability of breeding ponds.

Since the predictive framework in Chapter 2 was published (Martin & Murray, 2011), several studies have shed further light on the impacts of exotic plant invasions on amphibians. Alteration of habitat structure by the invasive shrub Amur Honeysuckle (*Lonicera maackii*) reduced ground-level temperature and humidity in forest sites of Missouri, USA. Amphibian species richness and evenness were lower in invaded forest than in uninvaded forest. Species composition also varied between invaded and uninvaded forest (Watling *et al*., 2011a). Further evidence has also emerged of exotic plants with novel features impairing amphibian reproductive success. Exotic plants with high concentrations of phenolics in their tissues impair tadpole development (Watling *et al*., 2011b; Cohen *et al*., 2012) by altering water chemistry as do exotic plants that alter C:N and N:P ratios of wetland leaf litter (Maerz *et al*., 2010; Cohen *et al*., 2012). European Buckthorn (*Rhamnus cathartica*), an exotic plant invading wetlands throughout the United States, releases the secondary metabolite emodin that has teratogenic effects on embryos of the native Western Chorus Frog (*Pseudacris triseriata*) (Sacerdote & King, in press).

The literature provided limited evidence to test the prediction that the impacts of exotic plants would be exerted most strongly on reptiles and amphibians exhibiting small body size. This highlighted the need for field investigations to determine the importance of body size in influencing reptile and amphibian sensitivity to the impacts of exotic plant invasion.

4. To test key model predictions through field investigation of the impacts of invasive exotic plants on reptile and amphibian assemblages.

Several key model predictions pertaining to the importance of exotic plant growth form and body size and diet of native reptiles and amphibians were tested by comparing the impacts of the invasive exotic plants Lantana (*Lantana camara*) and Bitou Bush (*Chrysanthemoides monilifera* ssp. *rotundata*). Lantana represented a growth from that was not prevalent in the dry sclerophyll forest it invades while Bitou Bush provided a similar growth form to the native vegetation it replaced in coastal heathland. I predicted that Lantana would produce stronger and more readily

detectable impacts on reptiles and amphibians than Bitou Bush and that impacts would be greatest on small-bodied reptile and amphibian species. Low numbers of amphibians recorded during sampling periods meant that these predictions could not be tested for amphibians. I was, however, able to test model predictions for reptiles.

In Chapter 3 I demonstrated that invasion of dry sclerophyll forest by Lantana was associated with significantly reduced reptile abundance and that this was driven specifically by reduced abundance of *Lampropholis delicata*, the smallest reptile species present. In contrast, invasion of coastal heathland by Bitou Bush was not associated with any significant impact on reptile abundance. Interestingly, I found evidence that Lantana was facilitating the entry of the scincid lizard *Bellatorias major* into dry sclerophyll forest, a habitat with which it is not normally associated.

In Chapter 5 I demonstrated that Lantana invasion of dry sclerophyll forest altered habitat structure by increasing understorey cover. This resulted in lower insolation and cooler leaf-litter temperatures than were recorded in uninvaded dry sclerophyll. In contrast, Bitou Bush did not significantly alter the structure of coastal heathland habitat and did not produce cooler and shadier conditions. I did not find evidence that either Lantana or Bitou Bush significantly reduced the abundance of invertebrate prey (see Chapter 6), suggesting that the differential impacts of these two exotic plant species on reptiles were attributable to their differing effects on habitat structure and opportunities for thermoregulation.

My results support the prediction that exotic plants exhibiting novel growth forms and structural features produce stronger ecological impacts on reptiles than exotic plants that are similar to existing plant growth forms. Further, the prediction that these impacts would be exerted most strongly on small-bodied reptiles was confirmed.

I was not able to confirm model predictions relating to exotic plant impacts on predator-prey interactions through field investigations as neither Lantana nor Bitou Bush altered the abundance or composition of leaf-litter invertebrate assemblages. However, evidence to support these predictions did emerge in my Chapter 2 literature review. Further supporting evidence has recently been provided by an investigation of

the impacts *Tamarix* ssp. invasion into riparian habitats in the Mojave Desert, USA. Abundances of native lizards and invertebrates were lower in monotypic stands of *Tamarix* ssp. than in mixed stands of *Tamarix* and native vegetation (Bateman & Ostoja, 2012). This provides correlative support for predictions that the impacts on predator-prey interactions will increase with coverage area of exotic plants.

Although predictions relating to impacts exotic plant invasion on reproductive success of reptiles and amphibians were not specifically addressed in my field investigations, it is possible that impairment of reproductive success may have contributed to reduced abundance of reptiles in dry sclerophyll forest invaded by Lantana. The cooler leaf-litter temperatures recorded in invaded habitats due to overshadowing by Lantana may reduce the suitability of potential nesting sites for oviparous species such as *Lampropholis delicata*, the species driving the difference in reptile abundance between invaded and uninvaded sites

5. To investigate minimally-invasive methods of marking amphibians for short-term studies.

The need to develop minimally-invasive techniques for studies where only short-term mark retention is required was identified as a significant ethical issue affecting amphibian research of the type undertaken in this thesis. Current techniques such as toe-clipping and implanted marks are important tools in many amphibian research programs. However, their expense and invasiveness may not be justifiable in short-term studies. A laboratory trial of minimally-invasive skin-staining techniques on striped marsh frogs (*Limnodynastes peronii*) (see Chapter 7) indicated that staining with gentian violet is a promising alternative to more invasive techniques for studies where long-term mark retention is not required.

8.2 Research significance and management implications

The research presented in this thesis has demonstrated that plant and animal life-history traits are important in determining the impacts of exotic plant invasions on native reptiles and amphibians. In particular, the extent to which exotic plants modify

habitat structure and heterogeneity strongly influences their effects on reptiles and amphibians. My work provides strong evidence that exotic plants with growth forms and structural features that are rare or absent in native vegetation will exert strong and readily detectible impacts on native reptiles and amphibians. I also found evidence to support my hypothesis that exotic plants displaying larger spatial coverage will exert stronger impacts than those with lesser spatial coverage. My work also provides compelling evidence that the body size of reptiles is an important influence on their sensitivity to exotic plant invasion.

These findings have important implications for the management of exotic plant invasions and conservation of native reptiles and amphibians. Identification of exotic plant traits most likely to exert harmful impacts on native fauna will allow finite resources to be allocated to the management of exotic plant species displaying those traits. Exotic plants with traits identified as less likely to exert harmful impacts may be assigned a lower management priority or, where positive benefits to native reptiles and amphibians are identified, prioritised for retention. Decisions as to whether to control or retain exotic plants will need to consider the growth form and coverage of plant species in question and life-history traits such as body size of the reptile and amphibian species present. These decisions will not necessarily be straightforward and may need to be made on a case-by-case basis, taking into account the exotic vegetation and native fauna present at each individual site as well as the possible impacts of available control methods. For example, evidence that Lantana may be providing refuge habitat for *Bellatorias major* needs to be balanced against the impacts I detected on other native reptile species such as *Lampropholis delicata*.

Given this multi-layered complexity of exotic plant-native animal interactions, there may be considerable benefit in conducting trial or pilot studies to ascertain the impacts (positive and negative) of exotic plant control prior to undertaking full-scale control programs. The M-BARCI study of the impacts of Bitou Bush control by spot-spraying with glyphosate herbicide presented in Chapter 4 provides an example of one such study and a basis for designing future trials.

Management decisions may also need to consider known or suspected impacts on other native fauna and native flora. In addition to providing new insights into the impacts of exotic plant invasions on reptiles and amphibians, the trait-based approach employed in this thesis offers a way forward for invasion ecology. Recent debate has centred on the wisdom of focusing on the exotic origins of non-native species. The approach adopted in this thesis, while not ignoring the 'exotic' nature of invasive non-native plants, focuses on their impacts on native reptiles and amphibians. Development and testing of trait-based models to predict the impacts of exotic plant invasions on other native taxa such as plants, invertebrates, birds and mammals would offer considerable benefits for understanding and managing those impacts. In turn, funding and labour could be directed toward achieving maximum biodiversity benefits.

8.3 Future research directions

It was not possible to test all aspects of the predictive framework presented in Chapter 2 in the course of a single research project. There remains, therefore, considerable scope for further research to test model predictions and refine my predictive framework.

The low number of amphibians recorded in this study prevented testing of model predictions for amphibians using fieldwork data. Testing these predictions should be viewed as a high priority given serious and widespread amphibian declines in recent years. Future studies should focus on comparing frog habitats such as streams and ponds subject to exotic plant invasion with uninvaded frog habitat. This should include recording frog microhabitat usage to determine whether exotic plants are being avoided or utilised as habitat by frogs. Structural features and microclimates of invaded and uninvaded habitats should be compared to determine mechanisms driving any observed impacts. Combining nocturnal and diurnal surveys is recommended to maximise the numbers of frogs detected. Nocturnal surveys were not practical in this study due to access constraints at a number of sites.

The reduced abundance of reptiles in dry sclerophyll forest invaded by Lantana when compared with uninvaded sites raises interesting questions regarding

microhabitat use of reptiles in invaded sites. In particular, do reptiles in invaded areas avoid microhabitats with high densities of Lantana while utilising as refuge habitat patches in which Lantana is absent or in low density? If reptiles are confined to microhabitats from which Lantana is largely absent then impacts of Lantana invasion might be expected to increase as Lantana spreads into native patches and coverage size/density increases. This should be investigated using trapping and movement studies to identify microhabitat preferences within invaded sites. These should be coupled with experiments to manipulate the composition of leaf litter to determine whether reptiles actively avoid Lantana leaf litter.

Additional studies comparing multiple exotic plant species are required to further test model predictions relating to the importance of growth form, structural features and coverage area in determining impacts on reptiles and amphibians. In this thesis my fieldwork focused on two exotic plant species with widely differing effects on habitat structure. Future research should be focused on additional exotic plant species with varying degrees of difference to native vegetation to determine if there is a critical level of habitat modification required before impacts become detectable. Equally, studying the impacts of individual exotic plant species that invade multiple habitat types would shed light on whether impacts are habitat specific and dependent upon the extent to which native vegetation in each habitat differed from the target exotic plant species.

Further research is also required to test the prediction that invasive exotic plants that are taxonomically distinct from native vegetation will exert stronger effects on herbivory and predator-prey interactions than those that are taxonomically similar to native vegetation. This will require comparison of multi-species sets of exotic plants and their impacts of abundance and foraging efficiency of native reptiles and amphibians. Additional studies are also required to determine whether impacts on foraging efficiency differ between dietary specialists and generalists. In my Lantana and Bitou Bush studies the majority of reptiles encountered were generalist insectivores with flexible foraging behaviours so I was unable to test predictions relating to dietary specialisation.

In analysing the impacts of Lantana and Bitou Bush on availability of invertebrate prey I identified the possibility that differences between prey size and body types of invertebrates between invaded and uninvaded habitats may be important. Further research, including comparisons of body sizes and types of invertebrates present between invaded and uninvaded sites, as well as analysis of reptile and amphibian stomach contents may be required to resolve this question.

There is also scope for research to test the prediction that impacts on predator-prey interactions may vary according to the age of exotic plant stands, given that the composition of invertebrate species present in invaded habitats can vary with time since introduction and stand age (Sax, 2002; Brandle *et al*., 2008; Nguyen, 2010). This would require identification of suitable exotic plant species with stands of known varying ages to allow comparison of abundance, species richness and composition of reptiles, amphibians and invertebrates among stands.

Further research is required to investigate the impacts of exotic plant invasion on reptile and amphibian reproduction in more detail. Specifically, detailed comparisons of assemblages between invaded and uninvaded areas utilising multiple exotic plant species of varying growth form, structural features and stand size are required to examine whether there are any consistent differences in the reproductive traits of species present. These include oviparity versus viviparity, choice of oviposition sites, life span/generation time and sex determination mechanisms (i.e. temperature or genotypic sex determination).

There also remains considerable scope for further development of minimally-invasive marking and recognition techniques for amphibians. This should include testing skin-staining with gentian violet on a range of amphibian species to assess its suitability for general amphibian use as well as testing additional dye types to determine their potential for producing longer lasting marks.

8.4 Conclusion

This thesis represents the establishment and test of the first predictive framework to describe the impacts of exotic plant invasions on reptiles and amphibians. I identified

life-history traits of invasive exotic plants and native reptiles and amphibians that are linked to strong and readily detectable impacts. Key predictions of the model were supported by a review of published literature and field investigations. The framework also provides a basis for determining future research priorities and management decisions. This thesis has therefore made an important contribution to invasion ecology and to the conservation of reptiles and amphibians.

Appendix 1. GLM results for modified analysis of reptile abundance and species richness in relation to invasion of dry sclerophyll forest by *Lantana camara*. Data for spring and summer surveys at two randomly-selected invaded sites were omitted to simulate loss of two uninvaded sites for these surveys. Significant *P* values are in bold. 'Condition' = invaded or uninvaded, 'Time' = autumn, spring or summer.

	Condition		Time		Condition*Time	
Abundance	$F_{1,19}$	*P*	$F_{2,19}$	*P*	$F_{2,19}$	*P*
Total	9.19	**0.01**	0.12	0.89	0.29	0.76
Lampropholis delicata	13.34	**< 0.01**	0.26	0.77	0.99	0.39
Total without *L. delicata*	0.12	0.73	0.21	0.82	0.69	0.51
Species richness	0.04	0.86	0.79	0.47	0.20	0.82

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