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Invasive non-native plants retain native mammal communities in novel ecosystems

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Submitted for the degree of Doctor of Philosophy

October 2013

THE UNIVERSITY
OF ADELAIDE
AUSTRALIA

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Table of Contents

Human-mediated environmental impacts are now so extensive and pervasive that many consider that the planet has entered a new geological epoch – the Anthropocene.

Driven by the need to find solutions to these emerging challenges, biodiversity conservation is entering a phase of prolific innovation… With this upheaval of new ideas, there is a genuine risk of the conservation community fragmenting into different schools of thought. In an attempt to minimize that risk, we introduce a conceptual framework that moves beyond established dichotomies and offers ways to reconcile conflicting perspectives.

(Kueffer & Kaiser-Bunbury 2013)

Abstract

Biological invasions are a major threat to native ecosystems globally, yet in some landscapes they can also have important positive effects on native biodiversity. For example, invasive non-native plants have the potential to act as ecological engineers in novel ecosystems by ‘creating’ habitat where it is otherwise lacking, thereby increasing the diversity and abundance of native fauna. Yet little is known of their net effect on population persistence. Understanding the impact of non-native plants on native fauna is becoming increasingly urgent for conservation management, particularly in degraded and novel ecosystems where the broad-scale removal of weeds could threaten native fauna populations and the ecological processes they contribute to. This thesis takes a local and global view to investigate the conservation conundrum of native fauna responses to non-native plants. It examines the effect of non-native blackberry on individual, population and community-level responses of small native mammals in native, hybrid and novel ecosystems before proposing a multi-scale framework to quantify the net effect of non-native plants on native fauna persistence.

The research was undertaken in the Mount Lofty Ranges of South Australia, a biodiversity hotspot that is considered a ‘canary landscape’ for temperate woodlands. The environmental decline seen here is expected to follow similar trends elsewhere. Blackberry (*Rubus anglocandicans*) is a non-native and highly invasive environmental weed that has been reported to provide habitat for native birds and mammals in the study region. The research was conducted as a multi-species study of small mammal responses to blackberry, with a particular focus on the nationally endangered southern brown bandicoot (*Isoodon obesulus*). Small mammal communities were surveyed for 11 consecutive seasons across 13 sites (7,500 ha) that represented native, hybrid and blackberry-dominated novel ecosystems of the region. A mixed modelling approach was used to quantify the net effect of blackberry on fauna responses at multiple scales, including: individual (reproduction and physiology); population (abundance, adult female density, and recruitment); and community (species richness, diversity and interspecific competition). To the best of knowledge, this is the first study on the impact of non-native plants on the recruitment and population persistence of native mammals.

Ten species of small mammals, including six native, were captured across 12,235 captures and 31,407 trap sessions. Blackberry was identified as an ecological engineer in blackberry-dominated novel ecosystems, where it retains diverse native mammal communities of yellow-footed antechinus (*Antechinus flavipes*; vulnerable), bush rat (*Rattus fuscipes*), brushtail possum (*Trichosurus vulpecula*; rare), short-beaked echidna (*Tachyglossus aculeatus*) and southern brown bandicoot (*Isoodon obesulus*; endangered). The abundance, density, dispersal and recruitment of bandicoots were also greatest in blackberry, with arthropod abundance and blackberry density the strongest positive predictors for recruitment of juveniles from source populations into the overall meta-population. The results confirm that non-native plants can act as ecosystem engineers in novel ecosystems and create critical habitat that supports mammal communities where they would otherwise become locally extinct.

Interactions between non-native and native species are increasing worldwide, and quantifying these complex dynamics is essential in order to successfully tackle the conservation challenges of the future. The final chapter of the thesis responds to this challenge by critiquing the traditional and emerging methods used in the empirical study, and synthesizing these with existing frameworks on non-native – native interactions. The thesis concludes by proposing two conceptual frameworks to: (1) inform future quantitative assessments of native fauna responses to non-native plants, and (2) guide restoration to retain positive ecosystem processes while reducing those that are harmful. Thus the research contributes to native fauna conservation in fragmented landscapes via both primary data collection for multiple species at multiple scales, and by suggesting frameworks to improve the effectiveness of restoration by prioritizing actions where non-native plants provide habitat for native fauna in degraded ecosystems.

Acknowledgements

Dedicated to

Enid
who taught us to observe and work with nature's rhythms for "less haste, more speed"

Ori
for embracing this journey and already living as a next-generation custodian for the Earth

---

This research was only feasible because of team work and the generous spirit of many.
To say it was a labour of love by the team would be a colossal understatement!
Thank you to everyone who has enriched this journey and helped to strengthen the outcome.

Starting from the very beginning when the seeds of the research were first sown, I pay tribute to Ryan Incoll's insightful ponderings: "is it possible those blackberry creeklines are helping bandicoot populations in the region?"

Andrew Claridge who introduced me to the beauty, importance and intriguing world of truffle fungi. Pam Catcheside, Thelma Bridle, Julia Haska, Tony Robinson, Teresa Lebel, Melissa Danks, Sandra Abell, Tom May, Sapphire McMullan-Fisher and Patrick O'Connor who've taught me so much about the interconnectedness of ecosystems, the critical role of fungi as indicator and driver of ecosystem health, and how much we still have to discover about biodiversity and how to conserve it.

Wayne Boardman, Ian Smith, David McLelland, Brian Matthews, Brian Rich, Linley, Lyn, Paula and the rest of the Zoos SA animal health team for sharing some very early mornings, supporting the project so generously, going the extra mile in collecting and processing the blood samples, and for opening my eyes to the power of combining our physiology and ecology toolboxes.

The many modelling mentors who have inspired, advised and supported me along the way. Tom van Dooren & Woolf at Foljouf, Gisela in Aachen, Jane Prider, Blair Grace and Peter Ward. Thanks especially to Steve Delean who has been an inspiration, encouragement and more recently modelling mentor and anchor man.

Friends and fellow members of the Sturt Upper Reaches Landcare Group Inc. for helping to keep this research grounded and focused on achieving 'real' outcomes to help local landholders who are doing their best for nature conservation.

Southern Brown Bandicoot Recovery Team in the Mount Lofty Ranges which guided, questioned and strengthened this research journey through advice, discussion and support. Thank you especially to Wendy Stubbs, Kirstin Abley, Pete Copley, Anthony Abley, Vicki-Jo Russell, Luke Price & Renae Eden.

All our wonderful volunteers who assisted with field and lab work. Thank you especially to Brian, Apu and Nat who shared the bulk of the field work and taught me so much. To the rest of you – it was only possible because you gave so much of your time, care and generous spirit. Thank you all…

Abbie Madden
Adam Bennett
Ailsa Enting-Hawke
Alan Burns
Alex Cave
Amanda McLean
Amelia Kuveke
Amity Alexander
Andrew Dawson
Andrew Murphy
Andrew Palmer
Angie Eads
Anna Douglas-Morris
Annie Kraehe
Apu Kadam
Ash & Rhys
Barb Packer
Bec Duffield
Ben Cullen
Brian Matthews
Bridget Wrenn
Cate Paull
Catherine King
Catherine Whitehead
Chris Whackett
Chris Madden
Claire Francis
Isla Madden
Keilan Madden
Corinna Byrne
Corinna Freytag
Damian Stam
Dani Boddington
Dave Sinclair
David Frahm
Emma Robinson
Emmett Wood
Gareth Telfer
Gaye Bourke
Graham Bald
Graham Olds
Hannah Ling
Hayley Vial
Heather Browett
Heather Cross
Ian Clark
Ilona Weir
Irulan Prowse
Jacques Klop
Jenna Hoffmann
Jenny D’Arcy
Jo Baulderstone
Jo Lee
Joel Driver
John Spiers
Joss Bentley
Julia Bignell
Julia Robinson
Julie Brookes
Julie Quimby
Karen Davis
Karen Harris
Karleah Trengove
Kate Delaporte
Katherine Wale
Katrina Watson
Kelly Pelgrim
Kimberley Hobbs
Laura Howie
Laura Ruykys
Lesley & Jan Vick
Liberty Olds
Linda & Lucas
Liz Millington
Luke McLean
Madeline Fletcher
Maia Berman
Margaret Clark
Mathieu McCann
Megan Iskov
Michael Melville
Michelle Le Duff
Michelle Smyllie
Milla Mihailova
Natalie Andrews
Olly Lipcer
Paul Every
Peter Bird
Racheline Jackson
Richard Goonan
Rosey H
Ruth Bell
Sam Buxton
Sandy Kalz
Sarah Maclagan
Sarah Mantel
Sarah Pearson
Scott Campbell
Shane White
Simon Bush
Steve Johnson
Symone Krimowa
Teja Hasani
Tim Dorman
Tim Heyward
Tom Hurley
Troy Mann
Verita Stewart
You-You Li

University of Adelaide student teams took on aspects of the project and made it their own. Thanks to the Conservation & Restoration III teams of Kimberley Hobbs, Heidi Neubauer, Caitlin Smart, Daniel Miller, Simon Cutts, Chelsea Tothill, Doug Berrigan & Tari Pawlyk. Thanks to Katie Eley and David Porublev, Animal & Veterinary Science, for the gastro parasitic work. Scott Whitters and the Rostrevor College lads helped with trap checks and installing mealworm trays. Green Corps teams led by Darren, Rachel, Dana and Rick saved the day when we needed help setting up new sites, lugging traps, and all hands on deck to check traps and keep animals safe.

Our generous hosts in the field: Della and Louise; Andrew, Liz and Irulan; Sandy and Jim Doig, the SA Water crew at Mount Bold; Jen Pitman and her dedicated team of Park Rangers. Thank you so much for sharing your patch so generously, giving us a home and research base, for sharing the long journey and the laughs. The Mud Hut will always be our bandicoot base.

The Carthew, Taggart and Paton research groups at University of Adelaide. Jo Lee who guided me through the first steps and taught me the value of multi-species approaches and keeping an eye on your results. Thank you especially to Amanda, Laura, Nik, You-You, Leah, Casey, Tim, Bec & Bec.

Thank you to my co-authors who have deepened and strengthened this research. It’s an absolute pleasure to work with you, and I look forward to future research collaborations together.

Chapter 2 – Susan M. Carthew, Kirsten Abley, Jane Prider, José M. Facelli and Steve Delean

Chapter 3 – Susan M. Carthew and Brian Matthews

Chapter 4 – Susan M. Carthew and David Paull

Chapter 5 – Susan M. Carthew

Thank you to my wonderful supervisors David Paull, José Facelli and Sue Carthew. David provided invaluable assistance in the early stages and has remained an inspiration throughout. José took me under his wing when I needed it, has broadened and strengthened the research with his ecological community perspective and invaluable advice on analysis, and given confidence in the research within the international research field. Sue, you are an inspiration and exemplary supervisor – everything I needed, and so much more. I will be forever grateful for all you have taught me in research and life.

Most of all, thank you to my beautiful boys Graham and Ori. Thank you for: carrying me along the way, putting up with a cottage full of hessian and catch bags, taking first steps along traplines, trap checks on Christmas day, reveling in the wonders of pouch young and joeys, always being positive and enthusiastic, and being the most wonderful support team I could have ever hoped for. I love you more.

Chapter 1 Introduction

1.1 Biodiversity conservation in human-altered ecosystems

Habitat loss and fragmentation are widely recognised as two of the most damaging forces impacting on ecosystems and biodiversity worldwide (Scott 2005; Rybicki & Hanski 2013). Some argue that together these are the primary driver of global biodiversity loss because of their impact on population dynamics and extinction risk (Lord & Norton 1990; Henle et al. 2004; Ewers & Didham 2006; Garden et al. 2006). While fragmentation may be caused by natural influences, anthropogenic forces also have great impact and are considered a major threat in conservation biology (Ewers & Didham 2006). There is growing evidence that biodiversity responds to these human-altered environments in complex and varying ways, and that human disturbance can have a significant impact (Fox & Fox 2000; Harrington et al. 2001; Marzluff & Ewing 2001; Michalski & Peres 2005). This is evidenced in one example by the response of faunal communities to forest clearance in the globally-recognised biodiversity hotspot of Madagascar. Reptile and small mammal communities were the most sensitive to forest disturbance and experienced 50% and 40% reduction in species richness respectively, while bird richness declined by 26%. Species with the widest geographic and dietary ranges proved to be the most resilient (Scott et al. 2006). Time since disturbance can also be a strong predictor of species diversity and relative abundance (Fox & Fox 2000). For example, decreasing time since human disturbance within remnant forest patches has been a key determinant of local extinction rates for Amazonian primates and carnivores in Brazil, with higher rates of extinction associated with more recent disturbance (Michalski & Peres 2005). Some of these species may still recover from the recent disturbance, while in other systems the opposite has been found where species may initially appear to be resilient and then experience an ‘extinction debt’ of delayed impact over time (Tilman et al. 1994; Paton et al. 2004; Lira et al. 2012).

Interestingly, moderate disturbances can sometimes have a beneficial effect (Pardini 2004; Seifan et al. 2012). In an Atlantic forest, for example, regenerating secondary forest provided important habitat linkages with greater vegetation complexity, and small mammal richness, than the surrounding mature forest (Pardini 2004). Several studies have found that some urban and disturbed peri-urban areas have the capacity to support native vertebrate and invertebrate fauna (Dufty 1994; Scott et al. 1999; Baker et al. 2003) by providing a range of natural and artificial habitat niches (Low 1999; Garden et al. 2006). In some instances, native fauna may be in higher densities in these human-altered landscapes than elsewhere (Statham & Statham 1997; Eymann et al. 2006). In Australia, the marsupial common brushtail possum (*Trichosurus vulpecula*) is one such species (Statham & Statham 1997; Eymann et al. 2006). Kühn et al. (2004) questioned whether such increased abundance results from access to different and/or more accessible resources in these altered environments, or whether it merely reflects the tendency for urbanisation to concentrate in areas of naturally high biodiversity such as coastal regions. Further research is needed for many species to identify whether they are surviving as remnant populations that are vulnerable to extinction in urban and peri-urban settings, or whether the human-altered landscape provides beneficial resources that enable them to persist at higher densities.

1.1.1 Novel ecosystems: non-native plants as threats and facilitators of biodiversity

Landscapes are being continuously transformed by local and global environmental change. Hobbs et al. (2009) argued that human disturbance is one of the major drivers of landscape change, that these changes are often rapid, and in some cases irreversible, but can accommodate altered yet still diverse biodiversity in some systems. They provided a conceptual framework of three ecosystem types that may arise from biotic (including invasion by non-native species) and/or abiotic (including climate shifts) change: historic, hybrid and novel systems. Historic ecosystems are defined as retaining largely intact biodiversity and ecological processes. These traits and processes remain largely unchanged in hybrid ecosystems, but most of the species are different from the historic assemblages. Novel ecosystems, on the other hand, are considered to have been transformed completely from their historic state and both their ecological traits and species composition are heavily altered beyond the historic range. As a result, the biota of novel ecosystems is therefore mostly non-native. This framework by Hobbs et al. (2009) provided the overarching structure for this thesis, and positioned the local interactions between non-native plants and native fauna into a broader context of hybrid and novel ecosystems in human-altered landscapes globally.

Further insight and context have been drawn from reviews on non-native – native interactions by Schlaepfer et al. (2011) and Rodriguez (2006). Schlaepfer et al. (2011) specified six ecosystem roles that have been identified in previous studies of the impact of non-native species: modifying habitat (e.g. providing alternative shelter and/or food for native species); ecosystem engineering; triggering restoration; preserving species; replacing the ecological role of locally extinct species; and other ecosystem services (e.g. pollination or bio-filtration). Native species in the system will respond to these functional roles in different ways, which may be a catalyst for further detrimental and/or beneficial effects for individual species, communities and the ecosystem as a whole. Beneficial facilitation can occur when non-native species replace, substitute, perform similar functional roles to natives, or indirectly interact with native species in some other positive way (Rodriguez 2006; Schlaepfer et al. 2011). In some circumstances these species can act within the ecological niche of native species that have been removed or degraded in the landscape (Society for Ecological Restoration 2004). Non-native species have the greatest positive effect when they provide critical resources, increase habitat quality, replace the function of a native species, or reduce competition or predation, and by doing so allow the remaining native species to persist or even flourish within an altered ecosystem (Rodriguez 2006).

Interactions between non-native and native species, within and between the altered assemblages that are sometimes triggered, take place at different scales and paces to sometimes create highly complex ecosystems (Ewers & Didham 2006; Banks-Leite et al. 2013). The importance of these differing scales of fauna responses to landscape variables is being increasingly recognized and examined. Single-level studies have been criticized for their limited view of the impact of ecological forces on fauna dynamics, such as obscuring or exaggerating population declines (Garden et al. 2006). More recent studies are increasingly identifying fauna responses at multiple ecological scales (Forman 1995; Paull 2003; Dunford & Freemark 2005; Garden et al. 2006; Raebel et al. 2012; Banks-Leite et al. 2013). For example, landscape characteristics in the areas between forest patches influenced species richness and abundance of forest birds in Canada, but the spatial scale of this impact varied with surrounding land use (Dunford & Freemark 2005). Similarly, different guilds of Atlantic birds responded uniquely to spatial scale, highlighting the importance of multi-scale approaches rather seeking a single optimum scale for investigations (Banks-Leite et al. 2013). It is therefore important to identify the various ecological scales at which the target species interact with their environment (Garden et al. 2006), and to manage species within the context of their community as well as more broadly across the landscape.

1.1.2 Fauna responses to the landscape matrix

While the disturbance spectrum of Hobbs et al. (2006; 2009) provided an overarching framework for this thesis at global and landscape scales, the matrix between historic and hybrid remnant patches was also an important focus. Fragmented landscapes have traditionally been categorised in binary terms of either high quality ’remnant’ or inhospitable ‘non-remnant’ habitat (Kupfer et al. 2006; Stoddard 2010). This singularly negative view reduces complex ecosystem processes to simplistic alternative states. There is growing awareness that the fragmentation sensitivity of species is affected by their response to the mosaic of all habitats within the landscape, including continuous remnants, small patches, the surrounding matrix and even isolated elements (Gascon et al. 1999; McIntyre & Hobbs 1999; Bennett et al. 2006). Matrix can be simply defined as the area between patches of remnant vegetation (Fischer et al. 2005), or the disturbed areas of a landscape (Lindenmayer & Franklin 2002; Kupfer et al. 2006). This broader definition recognises that the matrix takes a variety of forms in any landscape, is likely to contain habitat of varying quality, and may constitute the majority of the landscape in many settings (Kupfer et al. 2006). The matrix also plays a critical role in landscape processes as it can provide the greatest connectivity and exerts the greatest influence over landscape function (Forman 1995). From this perspective, the matrix incorporates novel ecosystems (Hobbs et al. 2006) as well as agricultural areas, plantations, residential zones, roads and other landscape components with varying configurations of native and non-native species. When the disturbed areas are a minor percentage of the landscape (i.e. largely historic ecosystems), the processes in the matrix are likely to be less important. This influence grows as the novel ecosystems and other altered areas of the matrix increase in proportion to the historic and hybrid remnant patches in the landscape (Kupfer et al. 2006).

The matrix surrounding native vegetation patches can have a significant influence on native fauna within the remnants (Baum et al. 2004; Dunford & Freemark 2005), as well as those living in the matrix itself. Species that are able to persist within fragmented landscapes may be primarily remnant-dwelling yet able to disperse through the matrix, may use the matrix sometimes to supplement remnant resources, or may have adapted to use the matrix extensively (Pardini 2004; Garden et al. 2006). Gascon et al. (1999) found that a high proportion of forest-dwelling bird, frog and small mammal species in the Amazon were detected within the matrix of cleared forest where it had been undisturbed for up to 15 years, and up to 25% were found there exclusively. The likelihood of a species persisting long-term in human-altered landscapes is dependent on its ability to tolerate or exploit matrix resources or to use them to access alternative sites (Kupfer et al. 2006; Scott et al. 2006). These resources may be complementary or additional to those available in remnants, and therefore have the potential to increase the resource base and habitat quality for species able to exploit them (Cook et al. 2004; Ewers et al. 2005; Fischer et al. 2005). For example, Santos-Filho et al. (2012) found the structural complexity of grasslands (cattle pastures) was the only consistent predictor for small mammal diversity and community abundance in south western Brazil, rather than characteristics associated with isolated forest remnants scattered throughout this pasture matrix. Similarly, the complexity, quality and permeability of vegetation in the matrix surrounding forest remnants were found to have a significant effect on forest birds in Canada (Dunford & Freemark 2005). Conversely, species that are unable to access matrix resources are more likely to decline or become extinct in remnants (Kupfer et al. 2006). It is therefore important to adopt a landscape-scale view to assess whether fauna are accessing and utilizing resources across their entire environment (McIntyre & Hobbs 1999).

Movement of individuals between habitat areas is influenced by the degree of connectivity in the landscape, which therefore plays a crucial role in maintaining populations and meta-populations (Fischer et al. 2005). Habitat connectivity across fragmented landscapes has traditionally been thought of in terms of wildlife corridors between remnant patches (Fischer et al. 2005). More recently, the impact of the surrounding matrix on connectivity and dispersal between remnant patches has been recognised (Pardini 2004; Fischer et al. 2005; Ashcroft & Major 2013). Fischer et al. (2005) found that birds used scattered trees as stepping stones between remnant woodland patches in south-eastern mainland Australia, while several reptile species used decaying logs and half-buried rocks for connectivity through the agricultural matrix surrounding the woodlands. Yellow-footed antechinus (*Antechinus flavipes)* have also been found to use the habitat matrix for inter-patch movements, enabling movement between populations and thus replenishment of local populations (Marchesan & Carthew 2004). The quality or permeability of the matrix is therefore a critical factor in determining the degree of functional connectivity between remnants (Pardini 2004).

A species' ability to persist in and exploit the matrix can be a key factor in determining its extinction proneness (Gascon et al. 1999; Pardini 2004; Fischer et al. 2005). Matrix connectivity is one of the major determinants of population persistence, and therefore needs to be taken into account when managing fauna populations within fragmented landscapes. A study on the impact of matrix habitat on birds in the hardwood forests of Ottowa, Canada, concluded that landscapes should be viewed as "integrated mosaics" of variable habitats that either facilitate or restrict a species' ability to persist (Dunford & Freemark 2005). Other studies have also confirmed matrix quality as a determinant of population persistence in remnants (Ricketts & Ritchison 2000; Fahrig 2001; Ewers & Didham 2006). This highlights the importance of combining population-level investigations with broader community-level assessments to understand interactions across the whole landscape mosaic (Dunford & Freemark 2005; Guenette & Villard 2005). The impact of different matrix components on native fauna populations across the disturbance spectrum needs to be better understood, particularly for fauna populations that are persisting within highly fragmented landscapes (Kupfer et al. 2006; Santos-Filho et al. 2012).

1.1.3 Fauna responses to habitat thresholds

The transformation of ecosystems from historic to hybrid and/or novel is non-linear, complex and involves transition through a number of ecological thresholds (Ewers & Didham 2006; Hobbs et al. 2009). These thresholds are tipping points in an ecosystem, where changes in the fundamental environmental conditions (e.g. available remnant area or quality of native versus novel habitat) can trigger dramatic changes in faunal communities and other biodiversity responses of a system (Suding & Hobbs 2009). Knowledge of ecological thresholds that identify the response of different species to ecosystem heterogeneity at various spatial scales is therefore needed.

Different species use different kinds of habitat and require different thresholds of habitat for persistence (Fahrig 2003). Recovery of threatened populations requires an understanding of how the characteristics of the landscape mosaic (e.g. habitat area, configuration and condition) impact on population dynamics, including extinction and re-colonisation processes (Wilson et al. 2001). This understanding can be strengthened when the tipping points for habitat characteristics, and their influence on fauna populations, are known at various ecological scales (Guenette & Villard 2005; Garden et al. 2006; Gooden et al. 2009). These thresholds can enable conservation strategies to be more targeted to the specific habitat needs of vulnerable species (Guenette & Villard 2005; Lindenmayer et al. 2005). Habitat thresholds may be particularly useful for managing novel ecosystems where there are complex interactions with native fauna persisting within them. Further research is therefore needed to identify and prioritise the habitat characteristics (e.g. total area, structural complexity, density) that act as critical upper and lower thresholds for native fauna persistence in novel ecosystems.

1.2 Blackberry and small mammal communities

Australia is one of only twelve mega-diverse countries in the world (Just 1998; Commonwealth of Australia 2009), and can be regarded as one of the two most biologically rich places on Earth (Williams & Whatman 2001; Yeates et al. 2003). Yet Australia is also known internationally for its extremely high rate of species extinction, with losses concentrated over the past two hundred years since European settlement. In this time, 25 species of plants, 23 birds, 4 frogs, and 27 mammal species or subspecies are thought to have become extinct *(*Commonwealth Government 1999). Clearance of native vegetation has been identified as the major cause of this ongoing biodiversity loss in Australia (Government of South Australia 2004). It has been estimated, for example, that the clearance of every 100 hectares of woodland results in permanent loss of habitat for up to 2,000 birds (Government of South Australia 2004). Rather than being addressed and halted, this loss of native vegetation and habitat has been accelerating throughout Australia. Land clearance in the past 50 years has matched clearance in the 150 years prior to 1945 (Government of South Australia 2004).

1.2.1 The Mount Lofty Ranges

The Mount Lofty Ranges are one of the most diverse regions in Australia and the most biologically rich in South Australia (Adelaide and Mount Lofty Ranges Natural Resources Management Board 2006; Department of the Environment and Heritage 2006). The Ranges cover approximately 5,300 km^2 and stretch 150km from Cape Jervis in the south to the Barossa Valley (Government of South Australia 2004). The region has a Mediterranean climate with a mean annual rainfall of 750 mm, hot summers and cool, wet winters (Wilson & Bignall 2009; Bureau of Meteorology 2012). Vegetation in the Ranges was historically dominated by woodlands in the high rainfall areas and grasslands and sedgelands in the lower lying areas (Adelaide and Mount Lofty Ranges Natural Resources Management Board 2006).

The Australian Government identified the Mount Lofty Ranges as a national biodiversity hotspot in 2003 because of its high number of endemic species combined with ongoing pressures of extensive vegetation clearance and degradation (Department of the Environment and Heritage 2006). Approximately 50 per cent of South Australia's native flora species occur in the Mount Lofty Ranges, and 45 of them are endemic (Adelaide and Mount Lofty Ranges Natural Resources Management Board 2006). This was one of the earliest landscapes to be cleared on a broad scale in Australia and is considered to be one of the most extensively cleared woodlands (Paton et al. 2004; Department of the Environment and Heritage 2006). McIntyre and Hobbs (1999) describe four landscape alteration states that have resulted from human-induced habitat modification and represent a continuum from intact to variegated, fragmented and relictual. With only 55,000ha (8%) of original vegetation remaining overall, the Mount Lofty Ranges represent a continuum of landscape alteration states with remnant patches in varying degrees of modification. The landscape mosaic ranges from fragmented areas, where native patches remain but have been modified, to relictual areas with isolated and mostly small native remnants (>100 ha) separated by a matrix of agriculture, semi-rural and peri-urban residential zones (Fig. 2.1; Paton et al. 2004). Many of the remnant patches are in poor condition due to habitat clearance and the invasion of non-native plants, such as blackberry and gorse (Paton et al. 2004) which are a major threat to biodiversity throughout Australia (Government of South Australia 2004). Nearly seventy non-native species have been proclaimed as pest plants in the region and are considered to be a significant risk to its environmental health (Adelaide and Mount Lofty Ranges Natural Resources Management Board 2006). The region is currently experiencing an 'extinction debt' as a result of this dramatic vegetation clearance and ongoing threatening processes (Szabo et al. 2011). Over 880 of the flora and fauna species present in the Mount Lofty Ranges are listed as

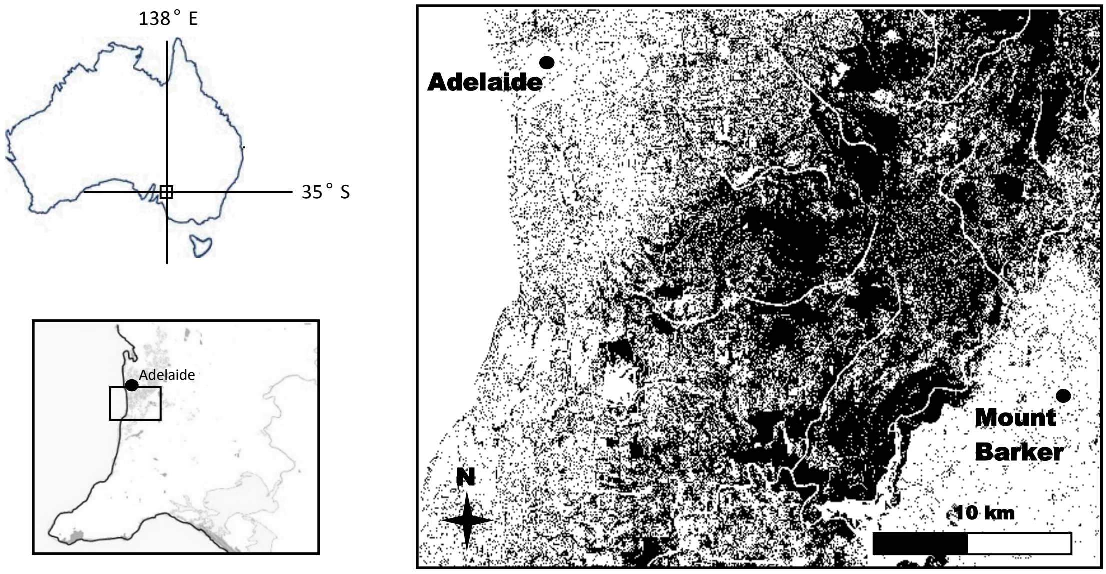


Figure 1.1 Map of the study region in the Mount Lofty Ranges of South Australia

Only 8% of remnant vegetation remains as relatively intact yet isolated patches. Major waterbodies are shown as white lines, and remnant native vegetation as large dark grey areas. Smaller areas of dark grey are remnant or introduced canopy, mostly with little or no understorey.

threatened at National, State and/or regional levels (Adelaide and Mount Lofty Ranges Natural Resources Management Board 2006). The Ranges, therefore, provide a useful study system because they are considered a 'canary landscape' for temperate woodlands in Australia, and potentially internationally; the environmental decline seen here is expected to follow similar trends elsewhere (Szabo et al. 2011).

1.2.2 Study species: blackberry (*Rubus anglocandicans*)

The *Rubus* genus in Australia includes 10 native and many non-native species from Europe, North America and Asia. Up to 16 species from the *Rubus fruticosus* aggregate, or European blackberry, were introduced from the early 1830s for hedgerows, gardens and to stabilize the banks of watercourses (Barker & Barker 2005; Victorian Department of Primary Industries 2009). As one of Australia's most invasive weeds, blackberry infests up to 9 million hectares along the east and south-west coast of Australia and, in 1999, was declared a 'Weed of National Significance' (NSW Department of Primary Industries 2010). Non-native blackberry presents a significant challenge for conservation management in Australia because it also provides food and shelter for native fauna such as the blue wren (*Malurus cyaneus*) and nationally endangered southern brown bandicoot (*Isoodon obesulus*) (Nias & Ford 1992; Paull 1992, 1995; Cochrane et al. 2003; Monks et al. 2005; Long 2010). Yellow-footed antechinus (*Antechinus flavipes*), bush rat (*Rattus fuscipes*), brushtail possum (*Trichosurus vulpecula*) and echidna (*Tachyglossus aculeatus*) have also been recorded in habitats where blackberry was present (Stewart 1979; Downes et al. 1997). Bush rat density has been found to increase in dense vegetation that included blackberry (Stewart 1979), and southern brown bandicoot and brushtail possums are known to consume blackberry fruits (Quin 1985; Cochrane et al. 2003; Monks et al. 2005).

In the Mount Lofty Ranges, the conservation conundrum of managing native fauna populations within blackberry habitat has become increasingly urgent (Gutierrez et al. 2007; Long 2010). *Rubus anglocandicans* is the most widespread European blackberry in Australia, including in the Mount Lofty Ranges (Evans & Weber 2003; hereafter referred to as blackberry in this thesis; Evans et al. 2007; Marshall 2008; NSW Department of Primary Industries 2010). This highly invasive blackberry can rapidly spread vegetatively with first generation canes spreading on average 3.3 m in one season, and 96% of these taking root and forming new plants in favourable conditions (Evans & Weber 2003). Blackberry has formed dense thickets along many waterways and drainage lines in the Mount Lofty Ranges, aided in its seed dispersal by non-native and native birds and mammals such as emu (*Dromaius novaehollandiae*), red fox (*Vulpes vulpes*) and southern brown bandicoot (Marshall 2008; Government of South Australia 2010). The southern brown bandicoot, in particular, is known to use blackberry as habitat in the Mount Lofty Ranges (Paull 1992, 1995; Long 2010). Although bandicoots and other small mammal species are known to exist in hybrid and novel blackberry habitats, it is unknown how blackberry resources compare with those available in the historic habitat of continuous forest or heathland, how the novel blackberry habitat impacts on small mammal communities and their persistence, or its effect on competitive interactions within small mammal communities.

1.2.3 Study species: small native mammal communities

This research was initiated because the government-led advisory group for southern brown bandicoot conservation in the Mount Lofty Ranges needed to understand why bandicoots were using blackberry, and whether it provided critical habitat and therefore needed to be managed differently. The resultant project was broadened to include the wider small mammal community (Fig. 1.1) for three reasons: (1) to integrate the needs of multiple species, (2) to investigate the ecosystem processes that small mammal communities contribute to, and (3) because small mammals can be useful ecological models and highlight trends within ecosystems more broadly. The rationale for each of these is outlined below.

Ecological research that focuses on a single-species and/or ecosystem can sometimes be limited in scope, impact and applicability. Significant limitations can include: potential conflict with the interactions and conservation requirements of other co-existing species or taxa; one-directional focus (e.g. solely positive or negative) rather than identifying net effects across a community or ecosystem; and hence an inability to offer conservation recommendations for the broader ecological community (Garden et al. 2006; Vitule et al. 2012). A multiple species approach is particularly important where habitat restoration is being considered, as these activities should focus on restoring resilience, species diversity and ecological processes rather than conserving a single species (Garden et al. 2006; Wortley et al. 2013). Investigations that include multiple species are challenging yet necessary if future restoration and conservation is to target the diverse habitat requirements of fauna communities (Guenette & Villard 2005).

The ecological services provided by small mammal communities, and the potential for these to be lost through broad-scale habitat clearance from inappropriate 'restoration' activities, were also a strong impetus to adopt a multi-species approach here. These beneficial services include soil improvement, seed and fungal dispersal, pollination, and food provision as prey

Fig. 1.1 The study species of small mammal communities in the Mount Lofty Ranges, South Australia

a) Southern brown bandicoot (*Isoodon obesulus*, photo by Les Peters b) yellow-footed antechinus (*Antechinus flavipes*, Corinna Byrne) c) bush rat (*Rattus fuscipes*, Tony Robinson d) brushtail possum (*Trichosurus vulpecula*, Judith Lydeamore) e) short-beaked echidna (*Tachyglossus aculeatus*, Les Peters).

(Lee & Cockburn 1985; Goldingay et al. 1987; Claridge & May 1994; Fleming et al. 2013; Valentine et al. 2013). Mammals that forage by digging create soil pockets and alter fine-scale biotic and abiotic conditions (Eldridge et al. 2012; Valentine et al. 2013). For example, one southern brown bandicoot can turn over and aerate more than 10 kg of soil per day (Valentine et al. 2013). Similar diggings by woylies (*Bettongia penicillata*), a rat-kangaroo, alter water filtration and the movement of soil nutrients (Garkaklis et al. 2003), and increase regeneration of native sandalwood (*Santalum spicatum*) in Western Australia (Murphy et al. 2005). Although short-beaked echidna (*Tachyglossus aculeatus)* and bandicoots are the main native mammalian diggers persisting in the Mount Lofty Ranges, bush rats and antechinus are also known to disturb soil while they are foraging (Eldridge & Mensinga 2007; Frazer & Petit 2007; J. Packer pers. obs.). The ecological processes that result from the persistence of these small 'ecosystem engineers' are particularly critical in the highly degraded novel ecosystems of the Mount Lofty Ranges, and include improving soil health, facilitating nutrient cycling by dispersing fungal spores, and promoting plant germination (Claridge & May 1994; Garkaklis et al. 2003; Murphy et al. 2005; Eldridge et al. 2012; Hulme et al. 2013).

Fauna communities can sometimes act as useful models for ecological processes within a system (Kelly 2010). Small mammals have the potential to fulfill this role as they are often abundant in ecosystems (Stenseth & Lidicker 1992) and have a high population turnover (eg. age to sexual maturity is often within months, high reproductive output, high rate of dispersal; Matthysen 2005; Singleton et al. 2005). Further, small mammals can respond rapidly to environmental change by taking advantage of fluctuations in resource availability (eg. population explosions in response to food availability after significant rainfall events; Previtali et al. 2009). By adopting a multi-species approach, it was hoped the thesis may assist conservation planning in the Mount Lofty Ranges by providing more integrated management of blackberry where it provides habitat for the southern brown bandicoot and co-existing small mammal species.

Southern brown bandicoot (Isoodon obesulus)

While this dissertation has been conducted as a multi-species study of small mammal communities, it has a particular focus on the southern brown bandicoot (*Isoodon obesulus*) because it was concern for this endangered species that was the catalyst and driving force for the research. The southern brown bandicoot belongs to the genus *Isoodon* (family Peramelidae), a group of small to medium-sized ground-dwelling marsupials with short tapered muzzles that are endemic to Australia. Three *Isoodon* species are currently recognised, including the southern brown bandicoot (*Isoodon obesulus*) which is the last remaining member of eight species from the Peramelidae family that once occurred in South Australia (Aitken 1979; Paull 1992, 1995; Friend et al. 2008; Long 2010). The sub-species *Isoodon obesulus obesulus* is listed as endangered under the *Environment Protection and Biodiversity Conservation Act 1999* (Commonwealth Government 1999) due to the threatening processes of introduced predators (especially foxes and cats) and habitat loss as the result of native vegetation clearance and modification combined with altered fire regimes. *Isoodon obesulus obesulus* is also listed as vulnerable under the South Australian *National Parks and Wildlife Act 1972* (Government of South Australia 1972).

Southern brown bandicoots exist within remnant forest, woodland and heathland in the Mount Lofty Ranges, as well as in highly degraded habitats that are increasingly being targeted for restoration (Paull 1992; Haby & Long 2005; Long 2010). It is well documented that their key habitat requirements include dense understorey (Paull 1992, 1995; Claridge & Barry 2000; Paull 2003; Long 2010; Haby et al. 2012) and the availability of invertebrates, hypogeous fungi, grasses, seeds and fruits as food resources for their omnivorous diet (Opie 1980; Quin 1985; Paull 1992; Mallick et al. 1998; Keiper & Johnson 2004). Bandicoot abundance is influenced by minimum temperature ranges and summer rainfall, and by the resulting availability of food resources (Paull 2003; Haby et al. 2012; Paull et al. 2013). Paull et al. (2013; see also Paull 2003) reveal that fragmentation affects the southern brown bandicoot at multiple spatial and time scales. However, it is not known how this species uses and persists in fragmented and degraded habitat at a fine scale. In the Mount Lofty Ranges the species is known to persist within thickets of introduced weeds, particularly blackberry, but the value of this novel habitat for bandicoot persistence is not known. There are many specific unanswered questions about the quality of blackberry habitat for the southern brown bandicoot. For example, does blackberry provide the full range of resources that bandicoots require, from food to shelter and reproductive requirements? Does it provide high-quality habitat that is a population source for dispersal of bandicoots between populations, or is blackberry masking a population sink or ecological trap for the endangered southern brown bandicoot?

Bush rat (Rattus fuscipes)

Four other small mammal species that are sympatric with the southern brown bandicoot in the Mount Lofty Ranges were included in this multi-species study: bush rat, common brushtail possum, short beaked echidna and yellow-footed antechinus.

The bush rat (*Rattus fuscipes*; family Muridae) is endemic to Australia and one of seven native rodents in the genus *Rattus*. This small (65–225 g), nocturnal mammal is relatively widespread and abundant in forest and coastal heath along the eastern and southern zones of Australia (Lindenmayer et al. 2008b; Menkhorst et al. 2008; Van Dyck & Strahan 2008). Bush rats require habitat with dense understorey (Robinson 1988; Van Dyck & Strahan 2008) and are often associated with *Xanthorrhoea* spp. (Frazer & Petit 2007). They are active diggers and mainly ground-dwellers, with burrows created for shelter during the day (Frazer & Petit 2007) and soil turned over while they are foraging, although they are also known to visit flowering *Banksia* species and assist with pollination (Goldingay et al. 1987). Their omnivorous diet includes fungi, grasses, seeds, fruits and arthropods (Robinson 1988; Claridge & May 1994; Van Dyck & Strahan 2008; Vernes & Dunn 2009). Bush rats are sensitive to land clearance and degradation throughout their range due to their preference for dense native vegetation, and hence limited dispersal ability between remnant patches (Lindenmayer et al. 1999; Bentley 2008; Menkhorst et al. 2008).

Common brushtail possum (Trichosurus vulpecula)

The common brushtail possum (*Trichosurus vulpecula;* family Phalangeridae) is an endemic, semi-arboreal marsupial that is the largest possum in Australia (1.2–4.5 kg; Van Dyck & Strahan 2008). It occurs in forest and woodlands across the northern, eastern and south-western regions of Australia. Brushtail possums are largely dependent on old trees with hollows for nesting, and are therefore vulnerable to inappropriate fire regimes and predation from introduced foxes and cats (Morris et al. 2008). They are mainly herbivorous and their natural diet consists of leaves, blossom and fruit (Dearing & Cork 1999; Van Dyck & Strahan 2008), although they are also known to consume some fungi in their diet (Claridge & May 1994). Common brushtail possums are listed as rare in South Australia (South Australia National Parks and Wildlife Act 1972, Government of South Australia 1972) and other parts of Australia because populations have declined in most areas where they have previously existed (Morris et al. 2008). In metropolitan areas the possum has overcome the loss of old trees and nesting hollows by adapting to shelter in buildings (Lunney & Burgin 2004), and is often abundant (Van Dyck & Strahan 2008).

Short-beaked echidna (Tachyglossus aculeatus)

The short-beaked echidna (*Tachyglossus aculeatus;* family Tachyglossidae) is endemic and the only species of echidna in Australia (Van Dyck & Strahan 2008). Echidna populations are currently secure and found in a diverse range of habitats throughout Australia (Van Dyck & Strahan 2008;

Australian Museum 2009). The echidna is the largest mammal (2–7 kg) in the fauna communities included in this study (Van Dyck & Strahan 2008). In addition to its unique physical appearance, the echidna has two other distinctive characters: it is one of only two egg-laying mammals (monotreme) in Australia and uses mechanoreceptors in its feet to detect its major food resource, ants and termites (P. Rismiller, pers. comm.). Echidna are prodigious diggers that can dislodge rocks, pull apart termite mounds and turn over soil in pits up to 25 cm in diameter (Eldridge et al. 2012).

Yellow-footed antechinus (Antechinus flavipes)

The yellow-footed antechinus (*Antechinus flavipes;* family Dasyuridae) was the smallest species included in the study. This small (35–55 g) carnivorous marsupial is endemic and widespread from north-eastern Queensland to south-eastern South Australia, as well as in south-western Western Australia. Yellow-footed antechinus are semi-arboreal and prefer a combination of structurally complex native vegetation of dense understorey combined with *Xanthorrhoea* spp. or tree hollows for nesting (Marchesan & Carthew 2004). They are mainly insectivorous, but their generalist diet also includes flowers, nectar and small vertebrate fauna (Van Dyck & Strahan 2008). This species is listed as vulnerable in South Australia (South Australian National Parks and Wildlife Act 1972, Government of South Australia 1972) due to vegetation clearance and predation from foxes and cats.

1.3 Research aims

The overarching aim of the research presented here was to investigate the effect of non-native plants on the persistence of native fauna in human-altered ecosystems. This investigation was undertaken in two parts. A quantitative assessment of native fauna responses to non-native plants in a fragmented landscape system, the Mount Lofty Ranges of South Australia, was undertaken and then modelled at community, population and individual levels across three scales. The findings and insights gained from this investigation were then used in a comparative analysis of different approaches to quantifying the impact of biological invasions on native biota, particularly non-native plants on native fauna. The thesis is therefore structured to address the broader research aims with:

i. an investigation of the influence of blackberry on fauna responses, particularly:
    - small mammal richness, diversity and abundance at microhabitat and site scale (Chapter 2)
    - health condition of the southern brown bandicoot at site and landscape scale (Chapter 3)
    - habitat quality and population persistence of the southern brown bandicoot at site and landscape scale (Chapter 4).

ii. development of a conceptual framework to guide quantitative assessments of the net effect of native fauna responses to non-native plants (Chapter 5) by:
    - undertaking a comparative analysis of individual, population and community assessments of native fauna and non-native plant interactions
    - synthesising existing frameworks with learning from the comparative analysis to develop a conceptual framework for quantifying non-native plant and native fauna interactions at multiple scales.

The thesis includes three data chapters, each adopting a different approach to address the central question of how native fauna respond to non-native plants. To allow comparison between the different approaches in the final chapter, five habitat characteristics were identified that are independent and important indicators of habitat quality for small mammals. These five characteristics are then modelled as explanatory variables throughout the thesis, with different dependent variables in each chapter to predict small mammal responses at multiple levels and scales. Chapter 2 examines the effect of non-native plants on small mammal communities, their species richness, diversity and abundance. Chapters 3 and 4 focus on the effect of blackberry on the most threatened species within these small mammal communities, the southern brown bandicoot. Chapter 3 explores the potential for physiology to detect early warning signs of population stressors in novel ecosystems by examining the effect of blackberry habitat on bandicoot haematology. Chapter 4 models individual and population-based demographic measures to investigate the effect of blackberry on habitat quality and persistence for southern brown bandicoot populations. Finally, Chapter 5 presents a review of existing conceptual frameworks on non-native and native interactions, details a comparative analysis of the contribution of the different methods used, and then presents two new conceptual models to inform decision-making regarding native fauna and non-native plant interactions. Chapters 2 to 4 are written as stand-alone papers to be submitted following thesis completion. These papers have been written with multiple authors in an active style and therefore refer to “our research”. The contribution of each author is outlined in the Acknowledgements section of this thesis. Some minor duplication of text in the Introduction and Methods sections of these publication style papers was unavoidable.

Chapter 2 Ecosystem engineering by non-native blackberry (*Rubus anglocandicans*) retains small mammal communities in novel ecosystems

2.1 Introduction

Invasive non-native plants are widely recognised as a major threat to native ecosystems globally, yet their interactions can range from negative through to beneficial (Stanley & Fowler 2004; Sax et al. 2007; Schlaepfer et al. 2011). The negative effects of invasive flora on invertebrates and birds is well documented, and understanding how to balance this with their sometimes beneficial role for these taxa is growing (Neilan et al. 2006; Sogge et al. 2008; Watts et al. 2012). In contrast, the potential for positive interactions, and how to balance these with weed threats, is not well understood for other taxa, including amphibians (Martin & Murray 2011; Watling et al. 2011; Pethiyagoda & Manamendra-Arachchi 2012; Rogalski & Skelly 2012), reptiles (Martin & Murray 2011; McDonald & Luck 2013) and mammals (Schiffman 1994; Longland 2012). Reviews by Crooks (2002), Rodriguez (2006) and Schlaepfer et al. (2011) identified a range of potential and realised beneficial roles for non-native plants, including ecosystem engineering and habitat creation for native invertebrates, birds and marine life. Non-native species that act as ecosystem engineers by directly modifying their environment have the greatest potential for positive flow-on effects within native ecosystems. In particular, those that increase vegetation complexity and density have the strongest facilitative effect as this tends to benefit native faunal richness and/or abundance (Crooks 2002; Castilla et al. 2004; Rodriguez 2006; Jones et al. 2010). Invasive *Tamarix* spp. and *Mimosa pigra*, for example, reduce floristic heterogeneity while increasing vegetation layers and density, and could be considered ecosystem engineers as they increase the abundance of some mammal species (Braithwaite et al. 1989; Longland 2012). The capacity to change vegetation characteristics through ecosystem engineering, and hence their potential influence on mammal communities, is unknown for most non-native plants. This knowledge gap poses significant challenges for conservation management because invasive plants targeted for eradication may have created habitat that is critical for fauna populations.

Understanding and harnessing the complex interactions between native mammals and invasive non-native plants, and particularly the drivers underpinning these, is critical for conserving species and restoring native ecosystems. Management of these non-native species is one of the most contentious issues in biodiversity conservation (Hobbs & Shackelford 2013). Davis et al. (2011) argued that conservation priorities need to be based on whether species provide benefits or harm to biodiversity and ecosystem processes, not on the origin of the species. This is perhaps most urgent for faunal populations persisting in highly degraded novel ecosystems dominated by non-native species. We define novel ecosystems as those where the species composition and ecological processes are so dramatically transformed from their pre-disturbance dynamics that they have formed new or ‘novel’ systems (Hobbs et al. 2009). Novel ecosystems primarily consist of introduced species and have undergone much more significant biotic (including invasion by non-native species) and/or abiotic (including climate shifts) change than either historic or partially transformed hybrid ecosystems. Restoration to a pre-disturbance state is considered to be difficult or impossible to achieve (Hobbs et al. 2009). Predicting the potential effect of restoration strategies, including rapid and broad-scale control of non-native plants, on native faunal communities persisting in these novel systems is important if we are to reduce harm while harnessing beneficial interactions (Stanley & Fowler 2004; Hobbs et al. 2006; Seastedt et al. 2008; Davis et al. 2011; Schlaepfer et al. 2011). Quantifying and predicting these impacts is highly challenging because it requires intensive demographic approaches such as mark–recapture of fauna (Krebs & Boonstra 1984; Vitule et al. 2012).

Further complexity is added by the different scales and paces at which fauna, including native mammal communities, respond individually and collectively to changes in their environment (Carslake et al. 2011; Di Stefano et al. 2011; Banks-Leite et al. 2013). For example, looking beyond individual sites to managing weed infestations as linkages between novel and remnant ecosystems has the potential to support dispersal and more resilient meta-populations. To the best of our knowledge, the effect of non-native plants on fauna persisting within novel ecosystems has not previously been investigated at multiple levels (e.g. functional group, community, population and/or individual) and scales (e.g. microhabitat, site and/or landscape) concurrently.

In Australia, the plant genus *Rubus* includes ten native and many introduced species from Europe, North America and Asia. As one of Australia's most invasive 'Weeds of National Significance', European blackberry (*R. fruticosus aggregate)* infests over 9 million hectares along the east and south-west coasts of Australia (NSW Department of Primary Industries 2010) The most widespread from this aggregate is *R. anglocandicans* (hereafter referred to as "blackberry"). It can spread rapidly with first generation canes spreading on average 3.3 m in one season and up to 96% of these forming new plants (Evans & Weber 2003; NSW Department of Primary Industries 2010). Blackberry also presents a significant conservation conundrum in Australia because it sometimes provides food and/or shelter for native fauna such as the blue wren (*Malurus cyaneus*), bush rat (*Rattus fuscipes*), common brushtail possum (*Trichosurus vulpecula*) and southern brown bandicoot (*Isoodon obesulus*) (Stewart 1979; Nias & Ford 1992; Paull 1992; Laurance 1994; Cochrane et al. 2003; Victorian Department of Primary Industries 2009; Long 2010; NSW Department of Primary Industries 2010).

Small mammal communities are known to be influenced by factors including vegetation complexity and density, tree density, coarse woody debris, and litter depth as these determine access to important food resources such as arthropods and fungi (Catling et al. 2000; Claridge & Barry 2000; Schmid-Holmes & Drickamer 2001; Holland & Bennett 2007; Fauteux et al. 2012; Haby et al. 2012; Lam & Maguire 2013). Blackberry has formed dense thickets along many waterways in the Mount Lofty Ranges. While blackberry may reduce floristic richness, it can also increase vegetation structure, complexity and density in ecosystems that are naturally open or have been degraded through clearing (Jones et al. 1997; Crooks 2002; Jones et al. 2010; Holland-Clift et al. 2011; Watling et al. 2011). In these areas where native vegetation is reduced or no longer present, dense blackberry thickets can sometimes act as substitute habitat for native fauna (Marshall 2008; Government of South Australia 2010). Although some small mammal species are known to use blackberry as habitat (Stewart 1979; Nias & Ford 1992; Cochrane et al. 2003), there is currently a lack of understanding on whether there are thresholds for the amount and density of blackberry that is needed to provide suitable habitat, and how blackberry resources compare with those available in native vegetation habitats. Furthermore, there is no existing knowledge of how blackberry habitat influences small mammal communities, their persistence, or their competitive interactions.

We investigated the influence of blackberry on the composition and interactions of small native mammal communities at two spatial scales along a gradient of blackberry density within native vegetation in the Mount Lofty Ranges of South Australia. Our intention was to provide insight into invasive plant – native fauna interactions to inform conservation planning for novel ecosystems where control of environmental weeds need to be balanced with biodiversity conservation. We aimed to answer three critical questions:

i. how do the abiotic and biotic characteristics that are associated with dense blackberry compare with those in remnant native ecosystems?

ii. what are the implications of these biotic characteristics as potential habitat resources for native fauna?

iii. what is the influence of blackberry on small mammal communities in terms of species composition, diversity, abundance and interactions across different spatial scales?

2.2 Methods

2.2.1 Study area

We investigated small mammal communities in the Mount Lofty Ranges of South Australia (-35°E, 138°N, Fig. 2.1) along a disturbance gradient from relatively intact native vegetation to highly degraded novel ecosystems that were dominated by blackberry. The region is recognised as a National Biodiversity Hotspot because the rich biodiversity is under threat, with only 8% of native vegetation remaining amidst a peri-urban population (Commonwealth of Australia 2009). There are significant conservation challenges in managing this landscape, including the need to balance human needs with restoring native vegetation and habitat for threatened fauna. The region has a Mediterranean climate with a mean annual rainfall of 750 mm, hot summers and cool, wet winters (Wilson & Bignall 2009; Bureau of Meteorology 2012). Sites were located within a 7,500 ha area that represents a mosaic of landscape states from fragmented to relictual (sensu McIntyre & Hobbs 1999) within agriculture and peri-urban residential zones (Paton et al. 2004; Government of South Australia 2008). Vegetation communities within the area were predominantly *Eucalyptus* associations and ranged from open forest to woodlands (Government of South Australia 2008).

Potential study sites were identified on the basis of forage-diggings of southern brown bandicoots, or other recent bandicoot records, as this was the primary study species (Paull 1992; Sanderson & Kraehenbuehl 2006). Thirteen sites were further selected by stratifying across a disturbance continuum (Fig. 2.2) represented by three site types: dense native vegetation within continuous forest that had minimal disturbance and nil or few blackberry plants ('native', n = 4); dense native vegetation that had been moderately disturbed and was interspersed with blackberry ('hybrid' based on definition by Hobbs et al 2009; n = 4); and highly disturbed sparse native vegetation dominated by extensive blackberry ('blackberry' "novel system" in Hobbs et al. 2009; n = 5). Despite comprehensive searches of the region, further replicates of the native and hybrid sites were not able to be identified. We minimised differences between sites whenever possible by locating all survey grids along drainage lines, ensuring the minimum size of blackberry thickets was 180 m by an average width of 30 m, and locating all sites at least 1 km apart for spatial independence. The native vegetation at all hybrid and blackberry sites had been disturbed >10 years previously and then abandoned or managed with minimal intervention. Novel blackberry sites tended to occur along drainage lines that had been extensively cleared over the past 150 years, particularly for timber logging and intensive agriculture (Government of South Australia 2008). As a result, novel sites were characterised by open areas of non-native grasses with scattered native trees and understorey dominated by extensive thickets of blackberry.

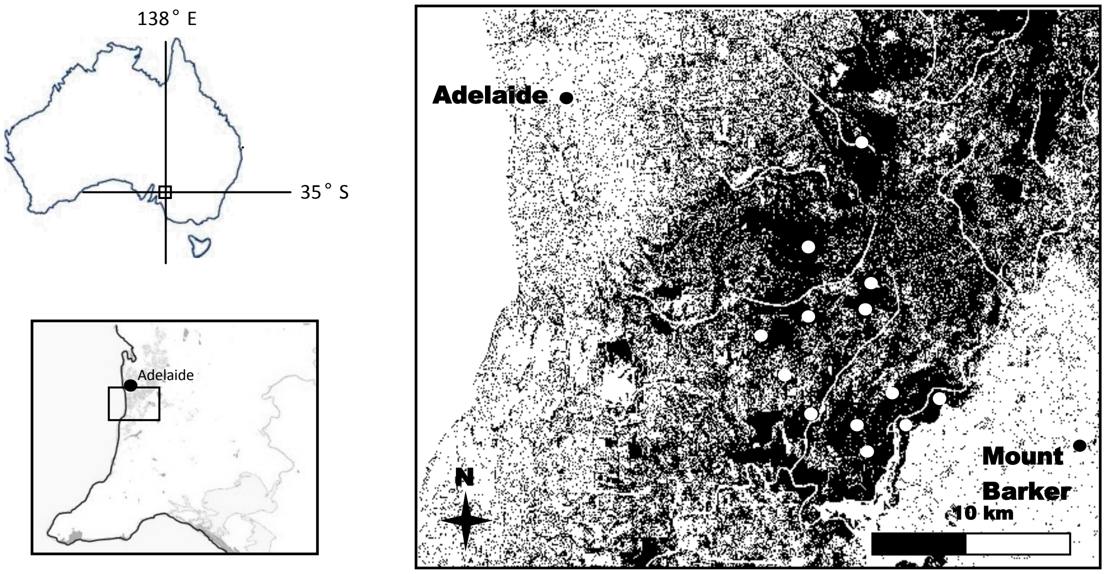


Fig. 2.1 Map of the 13 research sites within the Mount Lofty Ranges of South Australia

Only 8% of remnant vegetation remains as relatively intact yet isolated patches. The study sites are shown as white circles, major waterbodies as white lines, and remnant native vegetation as large dark grey areas. Smaller areas of dark grey are remnant or introduced canopy, mostly with little or no understorey.

Fig. 2.2 Details of the three site types

The three site types based on the disturbance spectrum of Hobbs et al. (2009): a) native site type with dense native vegetation; b) hybrid site type with dense native vegetation interspersed with blackberry along the drainage line; c) novel blackberry site type with sparse native vegetation dominated by blackberry along the drainage line, and Cape broom (*Genista monspessulana)* in the immediate foreground.

2.2.2 Small mammal surveys

Small native mammals were surveyed for 11 consecutive seasons (summer, autumn, winter, spring) between June 2008 and January 2011 to investigate the effect of blackberry on small mammal assemblages at the site scale. Our study species included three threatened species, the southern brown bandicoot (*Isoodon obesulus*, endangered, Environment Protection and Biodiversity Conservation Act 1999, Commonwealth Government 1999), yellow-footed antechinus (*Antechinus flavipes*, vulnerable, South Australia National Parks and Wildlife Act 1972, Government of South Australia 1972) and brushtail possum (*Trichosurus vulpecula*, rare, South Australia National Parks and Wildlife Act 1972, Government of South Australia 1972), and the more common bush rat (*Rattus fuscipes*) and short-beaked echidna (*Tachyglossus aculeatus*). These species range in mean adult body weight from 30 g in the case of the yellow-footed antechinus to 5 kg in the echidna, and in diet from the carnivorous yellow-footed antechinus to the mainly herbivorous brushtail possum (Dearing & Cork 1999; Van Dyck & Strahan 2008).

Each survey site consisted of two parallel 180 m long transects (Fig. 2.3). Transects at hybrid and blackberry sites were installed along either edge of the blackberry (DR) and all traps were placed under the canes. Transects were 30 m apart at native sites without blackberry, as this was the approximate mean distance separating the blackberry transects. Each transect had 10 trap stations placed 20 m apart. Each station consisted of one wire cage trap (600 mm x 260 mm x 240 mm) and one Elliott trap (Type A 33 x 10 x 10 cm). All traps were baited with a mixture of rolled oats, peanut paste and a small amount of linseed oil. Traps were set and checked in the morning and late afternoon during summer, autumn and spring, and in the morning during winter. Traps were opened from 5–7 nights per season, as traps were closed to safeguard animal welfare in extreme weather conditions.

During March–April 2010 we surveyed paired sets of parallel transects (DR and SL, Fig. 2.3) at nine of the sites (three from each site type) to investigate the effect of blackberry on small mammals at the microhabitat scale. Native and hybrid sites were selected for this component on the basis of reasonably dense native vegetation and consistently high small mammal captures during the prior seasons. At each site, one set of transects was placed along the drainage line (DR) as per the seasonal site scale surveys, and the second set of transects was placed 100 m away on the slope (SL) in native vegetation. Again, traps were open for 5–7 nights depending on weather conditions.

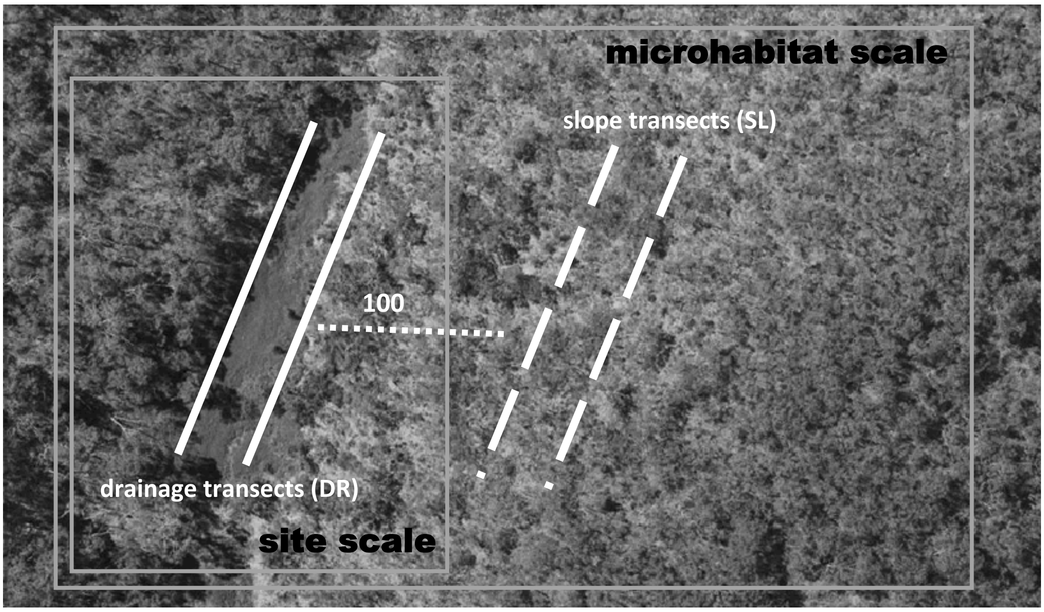


Fig. 2.3 Details of the survey transects

Spatial configuration of survey transects based on one blackberry site. Solid lines represent transects located along the drainage line (DR) – these were surveyed for 11 seasons at 13 sites to assess fauna responses at site scale. The heavy dotted lines represent the slope transects (SL) located 100 m from the drainage transects – these were surveyed for 1 season at 9 sites to assess fauna responses at microhabitat scale. Each transect was 180 m long and had 10 trap stations placed 20 m apart.

We were interested in the diversity and abundance of small mammal species in the blackberry compared with the surrounding native vegetation to determine whether blackberry was influencing the abundance of these species, and whether the same individuals were moving between the two habitats.

All captured animals were identified to species and released at point of capture. Southern brown bandicoot and yellow-footed antechinus were checked for reproductive condition as part of a more detailed investigation into the effect of blackberry on habitat quality for small mammals. Bandicoots, antechinus and brushtail possums were individually marked at their first capture. Because we caught large numbers of bush rats we recorded them as captures only, so that survey effort could focus on the threatened species. An echidna was only captured once at one site, so echidna diggings were instead surveyed in October 2010 and used to provide an indication of their presence. Echidnas were recorded as 0 (absent) or 1 (present) per site and included in the richness and diversity modelling.

2.2.3 Environmental surveys

Environmental and vegetation characteristics were recorded in October 2010. Site scale variables were measured at 13 sites (Table 2.1) by dividing trapping transects along the drainage lines (DR) into twenty 10 x 10 m plots and selecting five plots based on computer-generated random plot numbers. Plots at blackberry sites were positioned 1 m within the thicket to minimise any edge effect. For later analysis purposes, data for each site were averaged across the five plots. Vegetation complexity and density are useful indicators of potential shelter resources for native fauna, which in turn are important determinants of small mammal abundance (Catling et al. 2000; Haby et al. 2012). All vascular plant species within the plot were recorded, along with the number of individual *Xanthorrhoea semiplana* plants as they are known to be important shelter resources for the southern brown bandicoot and bush rat (Paull 1992; Frazer & Petit 2007; Haby et al. 2013). Pole surveys were conducted at ten points within each plot. Each point was selected by computer-generated random degrees and distances from the mid-point of the plot. We used a 2 m levy pole (1 cm diameter) divided into 25 cm increments and recorded the total number of touches (up to maximum of 10) for each plant species at each increment (Chaffey & Grant 2000). Vegetation density (VEG) refers to the mean number of total pole touches along the entire levy pole for each site. Blackberry density (BB) is the mean proportion of total vegetation density touches that were *R.* anglocandicans. Vegetation structure (STRUCTURE) is the mean number of pole increments with>10 touches of any plant species. The STRUCTURE variable is intended to be

Table 2.1 Description of environmental variables surveyed at site and microhabitat scale

Values for all variables were based on means across 5 randomly selected 10x10 m plots for each set of transects. Variables in bold were retained for subsequent explanatory habitat modelling.

	explanatory habitat variables
VEG	vegetation community
	native plant richness - mean no. of native plant species
	exotic plant richness - mean no. of exotic plant species
	vegetation density – mean pole touches 0 - 1.5 m
	vegetation density – mean pole touches 0 - 50 cm
	vegetation density – mean pole touches 50 cm – 1 m
	vegetation density – mean pole touches 1 - 1.5 m
BB	**pole touches by blackberry as % of veg density 0 - 1.5 m**
	blackberry area (m^2)
DBH	**mean diameter at breast height (cm) for trees >10 cm**
	canopy height (m)
	canopy % cover
	stags – mean no. individuals >10cm DBH
EWD	**mean pole touches of elevated woody debris (1-10cm diam) detached and trapped in vegetation**
	logs – mean no. >10 cm DBH and >1 m long
litter	**mean litter depth (mm)**
moisture	**soil moisture index (1 - 8) measured with soil probe**
	soil pH measured with soil probe
slope	degrees measured with inclinometer
aspect	N, S, E, W measured with compass
structure	number of vegetation strata with > 10 pole touches
xanth	*Xanthorrhoea semiplana* density – mean no. individuals

a measure of vegetation complexity based on the number of strata layers within the vegetation and the density of these layers (Catling & Burt 1995; Catling et al. 2002). Tree abundance (DBH) was calculated by measuring the mean pooled diameter at breast height of all individual plants >10 cm diameter. Elevated woody debris (EWD) is a measure of the mean number of pole touches by dead vegetation >10 mm diameter that was detached and caught in the vegetation (Mac Nally et al. 2001; Fauteux et al. 2012). Litter depth (LITTER) was the mean depth (mm) of fine litter <10 mm based on measurements taken at five points scattered throughout each plot.

To assess the effect of vegetation and environmental variables at the microhabitat scale we surveyed the second pair of trapping transects (SL) at nine sites using the same protocol as the site scale variables. In addition, we measured soil moisture (MOIST) on a categorical index from 1 (dry) to 8 (wet) at each paired transect. The soil moisture index was estimated using an agricultural soil conductivity probe designed to assess pH and moisture (Nutri-Tech Solutions METZD-05 www.nutri-tech.com.au). Measurements were taken at five points scattered throughout each plot at a probe depth of 8 mm. Preliminary trials were conducted to test the accuracy of the instrument against soil moisture content (volume of water present: total volume of soil sample) recorded by a HH2 Moisture Meter and ML2x ThetaProbe (Delta-T Devices Ltd, Cambridge UK). A generalized linear model with Poisson distribution and log link function, and post-hoc Tukey’s Honestly Significant Difference test, detected no significant difference between 50 random paired measurements taken over several days ($P < 0.001$). We chose this approach because it gave a more reliable and objective reading than Likert scale estimation, while still being rapid enough to allow for heterogeneity within plots by calculating the mean from multiple readings per plot.

2.2.4 Statistical analyses

A combination of generalized linear mixed models (GLMMs) and generalized additive mixed models (GAMMs: Wood 2006; Zuur et al. 2009; Crawley 2013) was used to investigate small mammal responses to blackberry and other habitat characteristics at the site and microhabitat scales. The use of GAMMs within an information-theoretic framework provided a powerful approach to explore complex relationships and ecological thresholds with non-linear responses, and to account for potentially systematic spatio-temporal variances resulting from repeated sampling over multiple sites and seasons (Burnham & Anderson 2002; Cunningham et al. 2005; Jensen et al. 2005; Zuur et al. 2009). GAMMs also addressed the zero-inflated and count-derived nature of the mark-recapture abundance data for our target mammal species (Zuur et al. 2012).

Exploratory data analysis was conducted to check for outliers, collinearity and relationships at the site and microhabitat scales. All 22 habitat variables were checked for collinearity using Pearson correlation coefficients (<0.60) and variance inflation factors (<2.00: Zuur et al. 2009; Zuur et al. 2012). The final set of five environmental variables (vegetation density, blackberry as % of vegetation density, DBH, elevated woody debris and litter) at the site scale and three variables (vegetation density, blackberry as % of vegetation density and moisture) at the microhabitat scale ensured the models met the recommended ratio of more than 10 records per parameter (Wintle et al. 2005; Zuur et al. 2012).

All analyses were conducted in the R statistical package version 3.0.0 (R Core Team 2013). GLMMs were generated using the extension package *lme4* version 0.999999.2 (Bates et al. 2013) and assessed with Tukey's Honestly Significant Difference (HSD) tests in the *multcomp* package version 1.2.17 (Hothorn et al. 2008). GAMMs were developed in *gamm4* version 0.1.6 (Wood 2012), then assessed and ranked with the *MuMIn* package version 1.9.5 (Bartoń 2013).

Site scale

Differences in environmental characteristics and small mammal abundance between site types were tested using GLMMs with post-hoc Tukey's HSD multiple comparison tests. Data were derived from all 13 sites. We generated GLMMs with site type as the explanatory variable, with Poisson distribution and a log link function for each variable that was count-derived (vegetation density, elevated woody debris, mammal species), and GLMMs with Gaussian distribution and an identity link function for the remaining variables (Zuur et al. 2009). Small mammal abundance data were based on eleven seasons, and were standardized to 100 trap checks for each site and season. Year and season were combined into an additional explanatory variable (year*season) to account for any systematic spatio-temporal variances resulting from repeated observations from the same site over the eleven seasons (Cunningham et al. 2005; S. Delean pers. comm.). We included site, year, and year*season as random factors in all models that tested for differences in fauna abundance between site types. All GLMMs were tested for significance with Tukey's HSD.

We investigated the variables responsible for the differences between site types using GAMMs. To examine community-level responses of small mammals, species richness and Simpson diversity index were estimated by pooling data across seasons for each site. GAMM models were then generated with Laplace approximation to explore the predictive power of environmental variables on species richness, Simpson diversity, and individual small mammal species. GAMMs were generated with Gaussian distribution and an identity link function for Simpson diversity, and with

Poisson distribution and a log link function for species richness and individual species (Zuur et al. 2009). Site, season, and year*season were included as random factors. Full GAMM global models with all explanatory variables for each fauna response were generated in MuMIn (Bartoń 2013), and then all of the potential variable combinations were tested and ranked using the *dredge* function in MuMIn. We used an information-theoretic approach and assessed the GAMM model rankings according to their weightings derived from Akaike's information criteria for small sample size (AICc; Burnham & Anderson 2002; Zuur et al. 2009). All strong models with $\Delta \leq 2$ are reported. Model goodness-of-fit provides a stronger indication of model predictive power than AICc as it provides information on the variance and overall model fit (Nakagawa & Schielzeth 2013). Goodness-of-fit was assessed by comparing R^2 values. We also generated GAMM models for each explanatory habitat variable against each fauna response to examine the predictive power of each combination individually. We were particularly interested in those that were not identified in the top-ranked models but which might provide insight into native–non-native interactions. Goodness-of-fit was again assessed for each individual GAMM, and models with $R^2 > 0.05$ are considered to adequately explain the model deviance and provide reliable predictions for the response (Sodhi et al. 2008). All *P* values were derived from these individual GAMM estimates unless stated otherwise. Smoothed terms were considered to be statistically significant when their *P* values were <0.05. We then plotted individual GAMMs to identify any non-linear relationships and significant thresholds between habitat characteristics and small mammal responses. GAMM plots are provided as a summary that includes R^2 values from the top-ranked models and significant *P* values from the individual GAMMs.

Preliminary modelling of yellow-footed antechinus and bush rat abundance revealed complex responses to the environmental variables. This preliminary modelling also suggested that interaction between these two species may influence their abundance. Additional GAMMs with Poisson distribution and a log link function were therefore generated to explore the interactions and potential interspecific competition between yellow-footed antechinus, bush rat, southern brown bandicoot and brushtail possum at the site scale.

Microhabitat scale

Differences in environmental characteristics and small mammal abundance between microhabitats within and across site types were explored using GLMMs, and tested for significance with post-hoc Tukey's HSD tests. Data were derived from the paired transects at nine sites. GLMMs were generated with transect as the explanatory variable, with Poisson distribution and a log link function for responses that were count-derived (vegetation density, mammal species), and GLMMs with Gaussian distribution and an identity link function for blackberry and moisture (Zuur et al. 2009). Small mammal abundance data were based on one season standardized to 100 trap checks for each site, and site was included as a random factor in the models. All GLMMs were then tested for significance with Tukey's HSD.

We investigated the predictive power of variables responsible for differences at the microhabitat scale using GAMMs, following a similar approach to that used at the site scale but with a different random structure. GAMMs were generated using Laplace approximation with transect as the explanatory variable to explore the effect of microhabitat on fauna responses. Gaussian distribution and an identity link function were used with Simpson diversity as the response, and Poisson distribution with a log link function for individual small mammal species as the response. Site and transect were included as random factors to allow for the correlation structure resulting from repeated measures between microhabitats within the same site. Full GAMM global models were generated for each fauna response in MuMIn (Bartoń 2013), then all of the potential variable combinations were tested and ranked using the MuMIn *dredge* function within an information-theoretic approach. All strong models with $\Delta \leq 2$ are reported. Individual GAMMs were then generated for the response of each fauna species to vegetation density, blackberry % and moisture. Goodness-of-fit was assessed for each individual GAMM based on deviance explained (R^2), and models with $R^2 > 0.05$ are considered to adequately explain the model deviance and provide reliable predictions for the response (Sodhi et al. 2008). *P* values were also calculated for each model. Each of these GAMMs were plotted to visualize the relationship between habitat characteristics and fauna responses, and to identify any significant 'tipping points' in these predictions. Finally, GAMMs were generated with Poisson distribution anda log link function for yellow-footed antechinus, bush rat and southern brown bandicoot as explanatory variables individually to predict their effect on the response of the other two species. These are presented as GAMM plots, with significant *P* values displayed for those with strong predictive power.

2.3 Results

2.3.1 Differences between environmental characteristics

At the site scale, vegetation characteristics were similar across the disturbance continuum although, as expected, native sites had significantly higher floristic richness and lower blackberry density (Table 2.2). Hybrid sites tended to have the densest and most structurally complex vegetation. This was due to the density of the largely intact native vegetation combined with minimal blackberry (blackberry density $\bar{x}$ = 20%). Blackberry infestations did not dominate the dense native vegetation at these hybrid sites, despite being present along >200 m of the drainage lines. In contrast, blackberry sites had been moderately to highly cleared and disturbed along the drainage lines and the remaining native vegetation had been outcompeted by dense blackberry as a result ($\bar{x}$ = 42% of total vegetation density). The novel habitat created by blackberry along the degraded drainage lines was surprisingly similar to dense native vegetation across all variables except floristic richness.

At the microhabitat scale, there was a clear contrast between blackberry and the surrounding native vegetation at hybrid and blackberry sites (Table 2.2). Vegetation density was highest where native vegetation was interspersed with blackberry at hybrid sites ($\bar{x}$ = 325.33 vegetation touches per plot), and significantly lower in native vegetation away from the blackberry at hybrid ($\bar{x}$ = 155.67, HSD P = <0.001) and blackberry sites ($\bar{x}$ = 114.67, HSD P = <0.001). Although hybrid sites had been considered to be 'dense native vegetation with blackberry', the native vegetation away from the blackberry was not actually any denser than the sparse native vegetation at blackberry sites (HSD P = 0.21316). Hybrid sites had both the wettest and driest soil. The soil was significantly moister in the drainage lines ($\bar{x}$ = 7.6 on 1–8 index) compared to the slopes ($\bar{x}$ = 4.3, HSD P = 0.002) at these hybrid sites, but neither were significantly different to either drainage or slope at the native and blackberry sites.

Table 2.2 Mean values of habitat differences at the site and microhabitat scales

Habitat characteristics at the site and microhabitat scale based on the mean no. of pole touches, or individual measures, and standard errors (SE). At the site scale (unshaded), surveys were conducted across 13 sites. At the microhabitat scale (shaded), paired surveys were conducted at 9 sites in the drainage line where blackberry was present at the hybrid and blackberry sites, and 100m away on the slope within native vegetation. At each site data from 5 replicate plots were pooled and then averaged. The total number of replicates per transect and site is given, with site then microhabitat replicates indicated for drainage transects. Different letters in superscript indicate statistically different groups between blackberry, hybrid and native sites as identified by generalised linear models with post-hoc Tukey Honestly Significant Difference (HSD) multiple comparison tests. Significant differences for the five variables that were subsequently modelled are indicated in bold.

	blackberry				**hybrid**				**native**			
	drain		**slope**		**drain**		**slope**		**drain**		**slope**	
	n = 25 / 15		*n = 15*		*n = 20 / 15*		*n = 15*		*n = 20 / 15*		*n = 15*	
	mean	*SE*	*mean*	*SE*	*mean*	*SE*	*mean*	*SE*	*mean*	*SE*	*mean*	*SE*
native plant richness	6.00 ^{a}	1.43			12.00 ^{a}	2.27			25.50 ^{b}	2.67		
	6.00 ^{a}	2.31	7.33 ^{a}	2.84	11.00 ^{a}	3.05	31.67 ^{a}	2.72	27.30 ^{b}	2.72	25.67 ^{b}	0.33
exotic plant richness	4.60 ^{a}	0.60			2.25 ^{b}	0.75			0.00 ^{c}	0.00		
	4.00 ^{ab}	5.77	5.33 ^{a}	1.20	2.00 ^{abc}	1.00	0.33 ^{c}	0.33	0.00 ^{c}	0.00	1.00 ^{bc}	0.57
VEG (touches)	**211.40 ^{a}**	**23.14**			**299.75 ^{b}**	**39.66**			**210.25^{a}**	**19.94**		
	244.33 ^{a}	**19.91**	**114.67 ^{b}**	**12.13**	**325.33 ^{a}**	**42.85**	**155.67 ^{b}**	**14.19**	**230.33 ^{ab}**	**43.98**	**215.67 ^{ab}**	**27.14**
BB (%)	**0.42^{a}**	**0.11**			**0.20 ^{ab}**	**0.07**			**0.00 ^{b}**	**0.00**		
	0.48 ^{a}	**0.14**	**0.00 ^{b}**	**0.00**	**0.13 ^{b}**	**0.05**	**0.00 ^{b}**	**0.00**	**0.00 ^{b}**	**0.00**	**0.00 ^{b}**	**0.00**
DBH (cm)	**33.40 ^{a}**	**16.38**			**87.50^{b}**	**6.79**			**78.50 ^{b}**	**28.93**		
EWD (touches)	10.60 ^{a}	1.96			6.50 ^{a}	1.85			10.00^{a}	1.96		
litter (mm)	3.75 ^{a}	0.73			4.07^{a}	0.54			2.76 ^{a}	0.72		
moisture (1 - 8 index)	**6.80 ^{ab}**	**0.49**	**5.15 ^{ab}**	**0.75**	**7.58 ^{a}**	**0.51**	**4.29 ^{b}**	**0.80**	**4.54 ^{ab}**	**1.07**	**4.80 ^{ab}**	**0.63**
slope (degrees)	9.60 ^{a}	3.80			18.00^{a}	4.06			17.25 ^{a}	1.97		
structure (no. layers)	5.40 ^{a}	0.75			7.50 ^{a}	0.50			5.20 ^{a}	1.03		

2.3.2 Small mammal differences and drivers at site scale

Ten species of small mammals were captured, including six native species, across 12,235 captures and 31,407 trap sessions (Table 2.3). There was significant heterogeneity in the abundance of individual species between site types. Southern brown bandicoots were most abundant at blackberry sites, with significantly more captures than at hybrid (HSD *P* = 0.043; Fig. 2.4) or native sites (HSD *P* <0.001). Of the four study species that were captured in sufficient numbers for statistical comparisons (i.e. excluding echidna), brushtail possums were the least abundant. There was no significant difference in possum captures between blackberry and hybrid sites (HSD *P* = 0.746). There were no captures of brushtail possums in native vegetation, which was significantly different to possum abundance at the blackberry (lower 99% confidence interval (CI) = 0.045) and hybrid (lower 99% CI = 0.027) sites. Yellow-footed antechinus and bush rats were present at all sites and in greatest abundance at the hybrid sites. However, there were no statistically significant differences between site types for either species.

Blackberry density was the only positive predictor for the persistence of small mammal communities at the site scale within the Mount Lofty Ranges (Tables 2.4 and 2.5). The diversity of these small mammal assemblages increased with the proportion of blackberry in the overall vegetation density (GAMM F = 6.70, *P* = 0.008; R^2 = 0.22), with no upper threshold detected in this relationship (Fig. 2.5). Of the four species, abundance of southern brown bandicoots (GAMM χ^2 = 11.67, *P* <0.001; R^2 = 0.24) and brushtail possums (GAMM χ^2 = 11.55, *P* = 0.003; R^2 = 0.28) were the most strongly predicted by blackberry density. Possum abundance plateaued when blackberry contributed above a threshold of 40% to the overall vegetation density. Bandicoot abundance was also positively correlated with the presence of elevated woody debris trapped in vegetation (GAMM χ^2 = 4.08, *P* = 0.043; R^2 = 0.03). Despite the prediction that small mammal diversity increased with blackberry density, yellow-footed antechinus were not individually influenced by blackberry or any other habitat characteristic at the site scale. Similarly, although bush rat captures tended to be higher at the hybrid sites this did not translate to blackberry as a positive predictor; bush rats were negatively predicted in the densest blackberry (GAMM χ^2 = 14.60, *P* <0.001; R^2 = 0.30).

The abundance of bush rats increased during the autumn season of March to July (GAMM *Z* = 12.29, *P* <0.001; R^2 = 0.10). Species richness and the diversity of small mammal communities also increased during autumn, as did the abundance of bandicoots and yellow-footed antechinus. However, the deviance explained by autumn for each of these models was nil or minimal (R^2 <0.05), so season was only a strong predictor for bush rat abundance.

Table 2.3 Abundance of small mammal species by site type

Total captures of all small mammal species from 11 seasons of mark-recapture surveys, based on 31,407 trap nights across 13 sites within the Mount Lofty Ranges, South Australia. The number of trap checks per site type is given for each site type. Small mammal abundance data were standardized to 100 trap checks for each site and season for subsequent modelling. Threatened species were marked individually and the total number of individuals per species and site type are given in brackets. * indicates an introduced species

	blackberry *n = 11781*	**hybrid** *n = 10223*	**native** *n = 9212*
common brushtail possum (*Trichosurus vulpecula*)	73 (18)	43 (12)	0
black rat *(Rattus rattus)**	575	268	167
bush rat *(Rattus fuscipes)*	1865	2561	2089
cat *(Felis catus)**	9	3	0
echidna (*Tachyglossus aculeatus*)	1	0	0
european rabbit *(Oryctolagus cuniculus)**	2	0	0
house mouse *(Mus musculus)**	173	53	14
common ringtail possum *(Pseudocheirus peregrinus)*	0	2	0
southern brown bandicoot (*Isoodon obesulus*)	1762 (176)	713 (88)	494 (56)
yellow-footed antechinus (*Antechinus flavipes)*	414 (112)	467 (119)	358 (78)
total captures of native fauna species	*4115*	*3786*	*2941*
TOTAL	**4865**	**4110**	**3122**

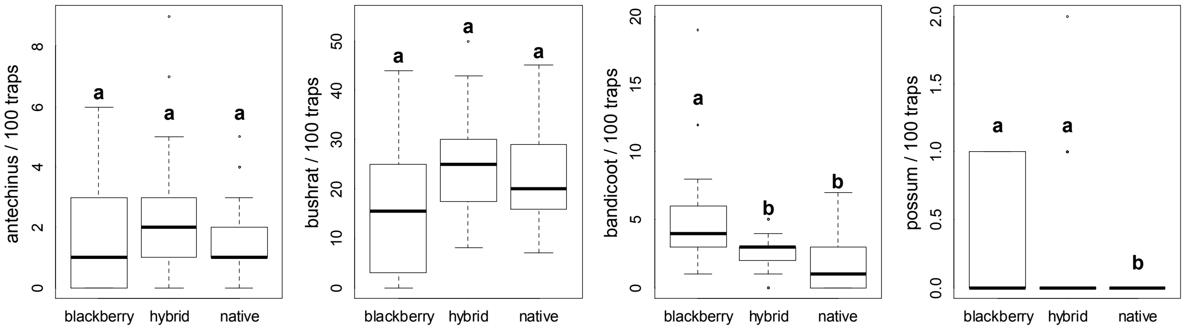


Fig. 2.4 Comparison of small mammal abundance at the site scale

Generalised linear mixed models (GLMMs) were generated for the abundance of each small mammal species ~ site type with site, season, and year by season as random factors. Bush rats are given as mean captures, the other species are mean individuals, and all are standardised to 100 trap sessions. GLMMs were then tested for differences between site types with post-hoc Tukey Honestly Significant Difference (HSD) test. Different letters indicate statistically significant differences.

Table 2.4 Top-ranked generalised additive mixed models (GAMMs) for native fauna responses to environmental variables

Full candidate GAMMs were generated with Laplace approximation for all non-collinear explanatory variables at the site and microhabitat scales, with site, season, and year by season as random factors. Simpson diversity was modelled with Gaussian distribution and an identity link function, and all individual fauna species with Poisson distribution and a log link function. Only the strongest models with Δ < 2.00 are presented.

site						microhabitat				
rank	*model*	*AICc*	Δ	*weight*	*R ^{2}(adj)*	*model*	*AICc*	Δ	*weight*	*R ^{2}(adj)*
community										
species richness										
1	NULL	39.18	0.00	0.43	0.00	NULL	18.80	0.00	0.86	0.00
2	DBH	40.84	1.66	0.19	0.11					
Simpson diversity										
1	NULL	162.98	0.00	0.58	0.00	NULL	39.96	0.00	0.90	0.00
2	BB	164.29	1.31	0.30	0.22					
individual										
bush rat										
1	BB + season	340.28	0.00	0.49	0.49	BB	62.15	0.00	0.82	0.00
brush-tail possum										
1	BB + veg	69.07	0.00	0.28	0.35					
2	BB	69.87	0.81	0.19	0.28					
3	BB + DBH	70.94	1.87	0.11	0.37					
southern brown bandicoot										
1	BB + EWD + litter	142.28	0.00	0.78	0.44	NULL	-14.02	35.76	0.00	0.00
2						BB	-11.18	37.37	1.61	0.27
yellow-footed antechinus										
1	NULL	149.57	0.00	0.29	0.33	NULL	30.69	0.00	0.78	0.00
2	BB	151.23	1.66	0.13	0.04					

Table 2.5 Generalised additive mixed model (GAMM) estimates for fauna responses to each environmental variable individually

GAMMs were generated with Laplace approximation for all non-collinear explanatory variables at site and microhabitat scale, with site, year, and year by season as random factors. Simpson diversity was modelled with Gaussian distribution and an identity link function, and species richness and all individual fauna species with Poisson distribution and a log link function. Site, year, and site by season were random factors at site scale, and site and transect were random factors at microhabitat scale. All test statistics are GLMM χ2 unless otherwise stated. Shaded variables were not modelled due to collinearity.

	species richness						**Simpson diversity**					
	site			**microhabitat**			**site**			**microhabitat**		
	test statistic	*R^2 (adj)*	*P*	*test statistic*	*R^2 (adj)*	*P*	*test statistic*	*R^2 (adj)*	*P*	*test statistic*	*R^2 (adj)*	*P*
season (March - May)	11.12 ^{z}	0.00	<0.001				11.70 ^{t}	0.03	<0.001			
VEG	0.27	0.01	0.606	2.39	0.40	0.220	0.00 ^{F}	0.00	0.988	**5.36 ^{F}**	**0.44**	**0.019**
BB	0.05	0.00	0.822	0.19	0.00	0.660	**6.70 ^{F}**	**0.22**	**0.008**	3.47 ^{F}	0.17	0.081
DBH	2.66	0.11	0.103				0.03 ^{F}	0.00	0.855			
EWD	0.06	0.00	0.811				0.00 ^{F}	0.00	0.977			
litter	0.14	0.01	0.707				0.15 ^{F}	0.00	0.697			
moisture				0.12	0.00	0.729				0.18 ^{F}	0.00	0.679

	bush rat						**brush-tail possum**			**southern brown bandicoot**						**yellow-footed antechinus**					
	site			**microhabitat**			**site**			**site**			**microhabitat**			**site**			**microhabitat**		
	test statistic	*R^2 (adj)*	*P*	*test statistic*	*R^2 (adj)*	*P*	*test statistic*	*R^2 (adj)*	*P*	*test statistic*	*R^2 (adj)*	*P*	*test statistic*	*R^2 (adj)*	*P*	*test statistic*	*R^2 (adj)*	*P*	*test statistic*	*R^2 (adj)*	*P*
season (March - May)	**12.29** ^{z}	**0.10**	**<0.001**				-4.04 z	0.01	<0.001	3.48 ^{z}	0.00	<0.001				2.09 ^{z}	0.02	0.036			
VEG	0.457	0.04	0.499	0.044	0.00	0.835	2.11	0.03	0.147	0.00	0.00	0.974	**8.19**	**0.29**	**0.014**	1.10	0.04	0.295	**5.15**	**0.22**	**0.038**
BB	**14.60**	**0.30**	**<0.001**	**17.15**	**0.00**	**<0.001**	**11.55**	**0.28**	**0.003**	**11.67**	**0.24**	**<0.001**	**21.95**	**0.63**	**<0.001**	2.82	0.04	0.093	0.72	0.01	0.550
DBH	2.76	0.00	0.097				0.25	0.01	0.620	1.10	0.06	0.294				4.06	0.07	0.099			
EWD	0.07	0.00	0.793				0.81	0.03	0.560	**4.08**	**0.03**	**0.043**				0.25	*0.00*	0.620			
litter	0.81	0.11	0.565				0.01	0.00	0.909	0.09	0.00	0.762				0.79	0.04	0.475			
moisture				1.649	0.00	0.239							1.46	0.14	0.237				0.04	0.00	0.840

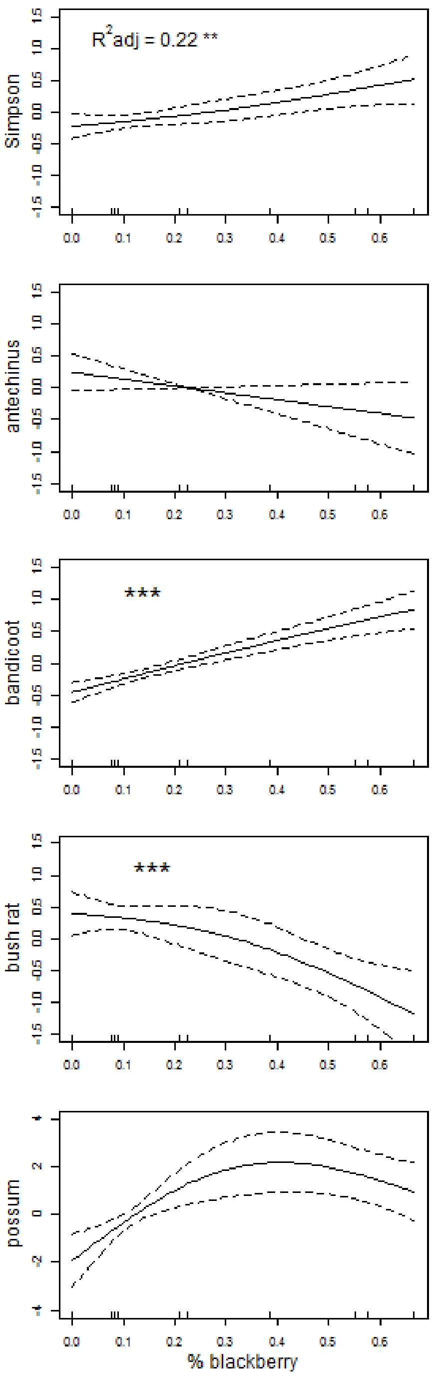


Fig. 2.5 Generalised additive mixed model (GAMM) plots of native mammal responses to habitat at the site scale

The plots give the estimated smoothing curves for GAM models of fauna abundance in response to explanatory habitat variables, with site, year, and year by season as random factors. Bush rats were modelled as mean captures, the other species as mean individuals, and all are standardised to 100 trap sessions. y axis is the smoothing effect of explanatory variables showing no collinearity on fauna response. The tick marks, or 'rug plot', on the x-axis represent the no. of individuals or captures; dashed lines are the ±2 SE (95%) confidence intervals. p values and R^2 scores are given for significant relationships. R^2 is the R^2 adjusted score, or % of data variability explained by the GAMM, and is stated if the explanatory variable was specified individually in the top-ranked GAM models in Table 2.4. * $p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$ are based on Table 2.5 estimates from additional GAMMs calculated for each explanatory variable individually.

2.3.3 Small mammal differences and drivers at the microhabitat scale

Paired trapping grids revealed significant differences in the way that small mammals respond to diverse vegetation communities within native, hybrid and novel sites. Bush rats, southern brown bandicoots and yellow-footed antechinus all responded at the microhabitat scale to the habitat resources available within their environment. The most striking contrasts were within the novel blackberry-dominated sites, where bush rats were more abundant in the blackberry drainage lines ($\bar{x}$ = 8.67±7.17) than in the surrounding native vegetation ($\bar{x}$ = 0.33±0.33), as were bandicoots ($\bar{x}$ = 5.00±1.00 in blackberry compared to 0.00±0.00 in native vegetation) and antechinus ($\bar{x}$ = 1.33±0.38 in blackberry compared to 0.00±0.00 in native vegetation) (Fig. 2.6). The nil captures of antechinus away from the blackberry-dominated drainage lines within those sites differed significantly from all other transects including blackberry drainage (lower 99% CI = 0.280), hybrid slopes (lower 99% CI = 0.280) and native slopes (lower 99% CI = 0.410). Likewise, the nil captures of bandicoots away from the drainage lines of blackberry sites was different to all other transects including hybrid slopes (lower 99% CI = 0.080) and native drainage lines (lower 99% CI = 0.436). This contrast was also present within the hybrid sites, although to a lesser extent. Bush rats were significantly more abundant in blackberry ($\bar{x}$ = 25.00±2.65) than 100 m away in the native vegetation ($\bar{x}$ = 9.33±1.33) of hybrid sites, as were bandicoots ($\bar{x}$ = 3.00±0.58 in blackberry compared to 0.67±0.33 in native vegetation). At the native sites there were no significant differences between small mammal captures along the drainage lines compared with 100 m away on the slopes in native vegetation (Fig. 2.6).

Overall vegetation density was the strongest positive predictor for the diversity of small mammal communities across all sites and transects (GAMM F = 5.36, $P = 0.019$; $R^2 = 0.44$; Table 2.4, Table 2.5, Fig. 2.7). Vegetation density was also a positive predictor of antechinus abundance (GAMM $\chi^2 = 5.15$, $P = 0.038$; $R^2 = 0.22$). While bandicoot abundance increased with overall vegetation density (GAMM $\chi^2 = 8.19$, $P = 0.014$; $R^2 = 0.29$), the proportion of blackberry within the vegetation was the strongest positive predictor (GAMM $\chi^2 = 21.95$, $P < 0.001$; $R^2 = 0.63$). Both Simpson diversity and bandicoot abundance reached a threshold around vegetation density of 300 (touches on levy pole per 10 x 10 m plot) and then flattened to neither a positive nor negative relationship above this threshold. In contrast, bush rat abundance was negatively correlated with blackberry density across all sites (GAMM $\chi^2 = 14.60$, $P < 0.001$; $R^2 = 0.30$), although within hybrid and blackberry sites the species was significantly more likely to be captured within blackberry than in the surrounding native vegetation. By using a mixed modelling approach, we were able to separate between the abiotic (moisture) and biotic (vegetation density, and blackberry as proportion of this density) influences on small mammal communities. Although blackberry thickets were concentrated

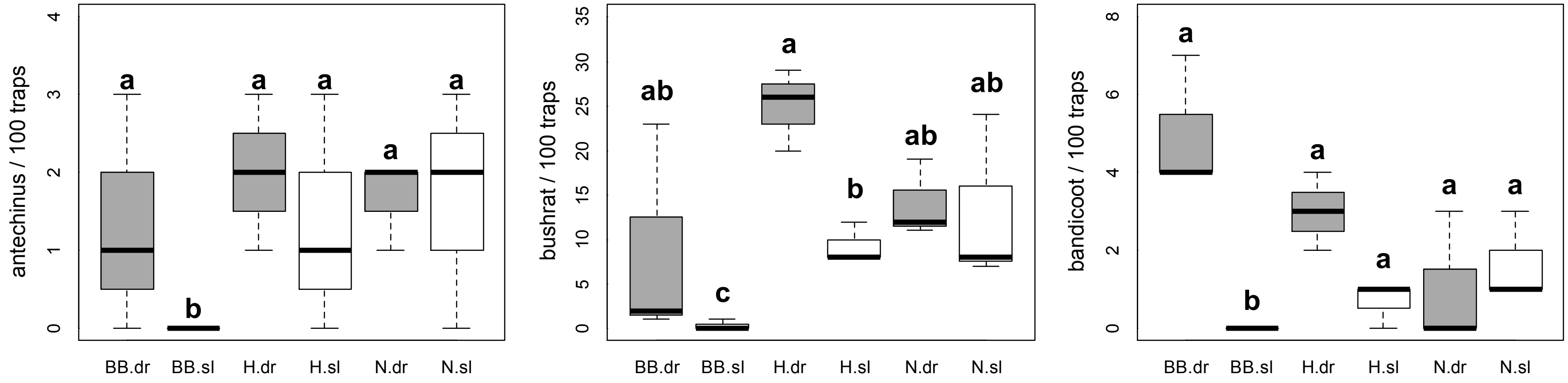


Fig. 2.6 Comparison of small mammal abundance at microhabitat scale

Generalised linear mixed models (GLMMs) were generated for the abundance of each small mammal species ~ site type by transect with site as random factor. Bush rats are given as mean captures, the other species are mean individuals, and all are standardised to 100 trap sessions. GLMMs were then tested for differences between site types with post-hoc Tukey Honestly Significant Difference (HSD) test. 99% confidence intervals were calculated to check for significant differences between the 0 captures of antechinus and bandicoots at blackberry slope transects compared to all other transects. Different letters indicate statistically significant difference between transects.

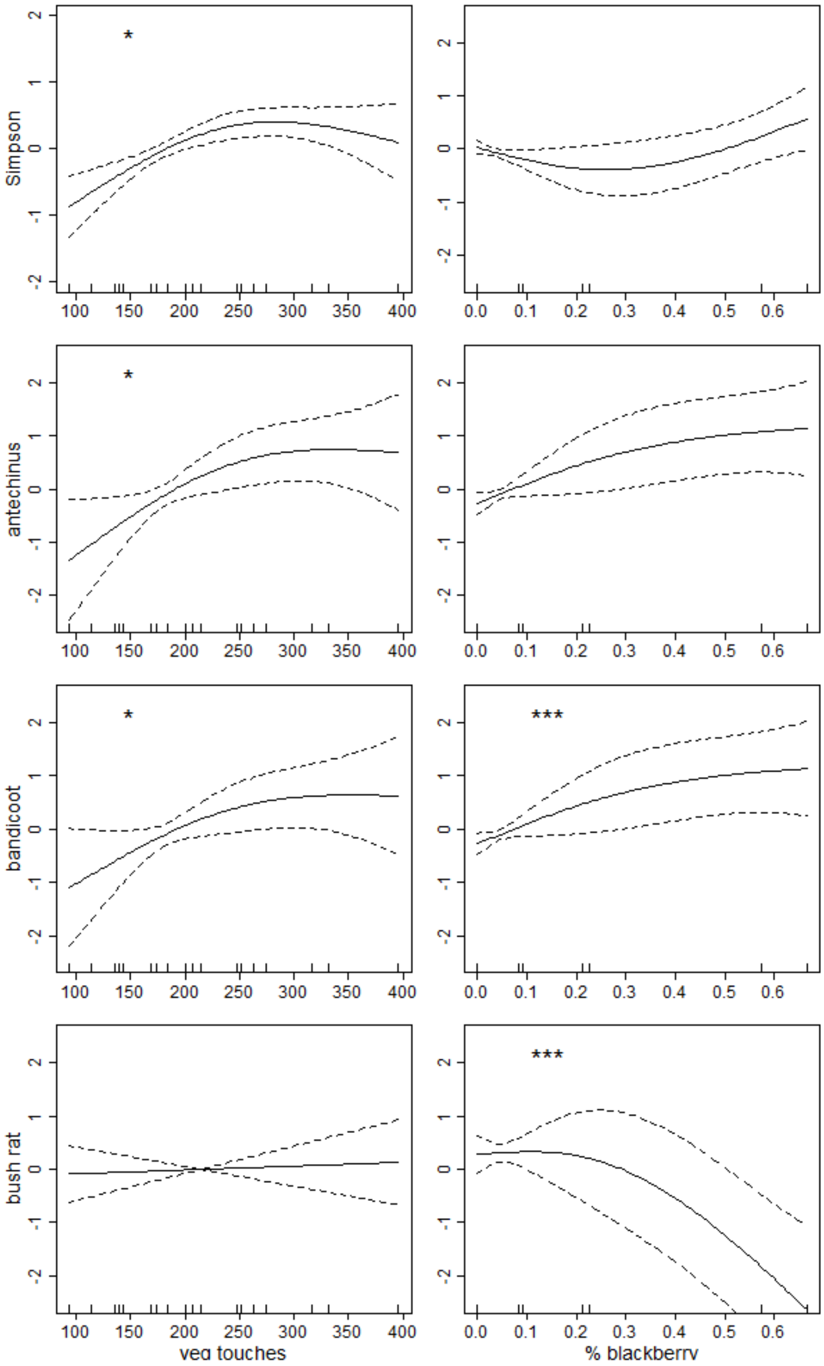


Fig. 2.7 Generalised additive mixed model (GAMM) plots of small native mammal responses to habitat at the microhabitat scale

The plots give the estimated smoothing curves for GAM models of fauna abundance in response to explanatory habitat variables, with site and transect as random factors. Bush rats were modelled as mean captures, the other species as mean individuals, and all are standardised to 100 trap sessions. R^2 is the R^2 adjusted score, or % of data variability explained by the GAMM, and is stated if the explanatory variable was specified individually in the top-ranked GAM models in Table 2.4. * *p* ≤0.05, ***p*≤0.01, ****p*≤0.001 are based on Table 2.5 estimates from additional GAMMs calculated for each explanatory variable individually. Refer to Fig. 2.4 for more details on the interpretation of GAMM plots.

along the moist drainage lines of hybrid and novel blackberry sites, moisture was not a significant predictor for small mammal diversity (GAMM F = 0.18, $P = 0.679$; $R^2 = 0.00$) or individual species.

2.3.4 Fauna responses and competition across landscape scales

Small mammal communities responded differently at the site and microhabitat scales. As shown above, species diversity was significantly influenced by overall vegetation density at the microhabitat scale (GAMM F = 5.36, P = 0.019; $R^2 = 0.44$), whereas it was blackberry in particular that predicted small mammal diversity (GAMM F = 6.70, $P = 0.008$; $R^2 = 0.22$) across the study region.

Interactions between mammal species were evident at both scales (Figs. 2.8 and 2.9), although the predictions were strongest at the microhabitat scale where individuals co-existed within the confines of blackberry at hybrid and blackberry sites. Bush rats and yellow-footed antechinus positively predicted the presence of each other at site scale, and this prediction strengthened at the microhabitat scale (bush rat GAMM $\chi^2 = 28.9$, $P < 0.001$, $R^2 = 0.43$; antechinus GAMM $\chi^2 = 10.51$, $P = 0.004$, $R^2 = 0.54$). Similarly, bandicoot abundance was a strong positive predictor for bush rats at site scale, and even more so at the microhabitat scale (GAMM $\chi^2 = 15.83$, $P < 0.001$, $R^2 = 0.40$). This relationship was not reciprocated as bush rats did not predict bandicoot abundance at either scale.

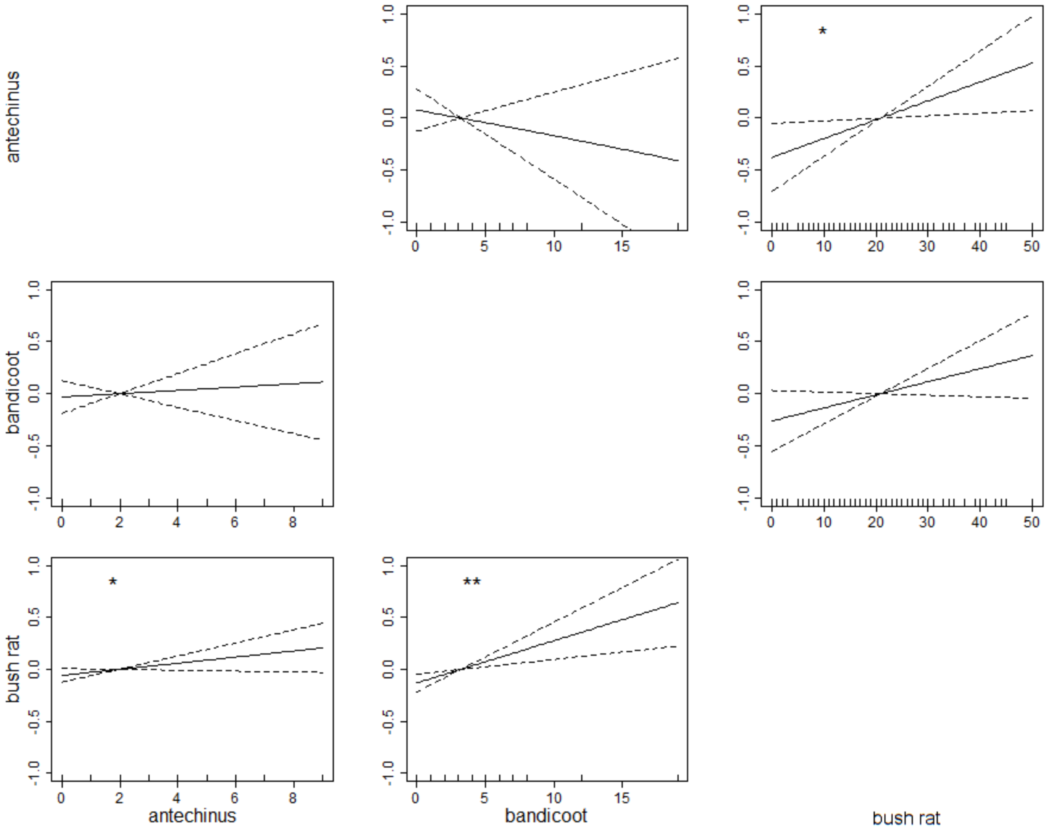


Fig. 2.8 Generalised additive mixed model (GAMM) plots of interaction amongst native mammals at the site scale

The plots give the estimated smoothing curves for GAM models on the abundance of individual fauna species in response to other fauna species. All GAMMs were modelled with Poisson distribution and a log link function, with site, year, and year by season as random factors. Bush rats were modelled as mean captures, the other species as mean individuals, and all are standardised to 100 trap sessions. **p* ≤0.05, ***p*≤0.01, ****p*≤0.001. Refer to Fig. 2.4 for more details on the interpretation of GAMM plots.

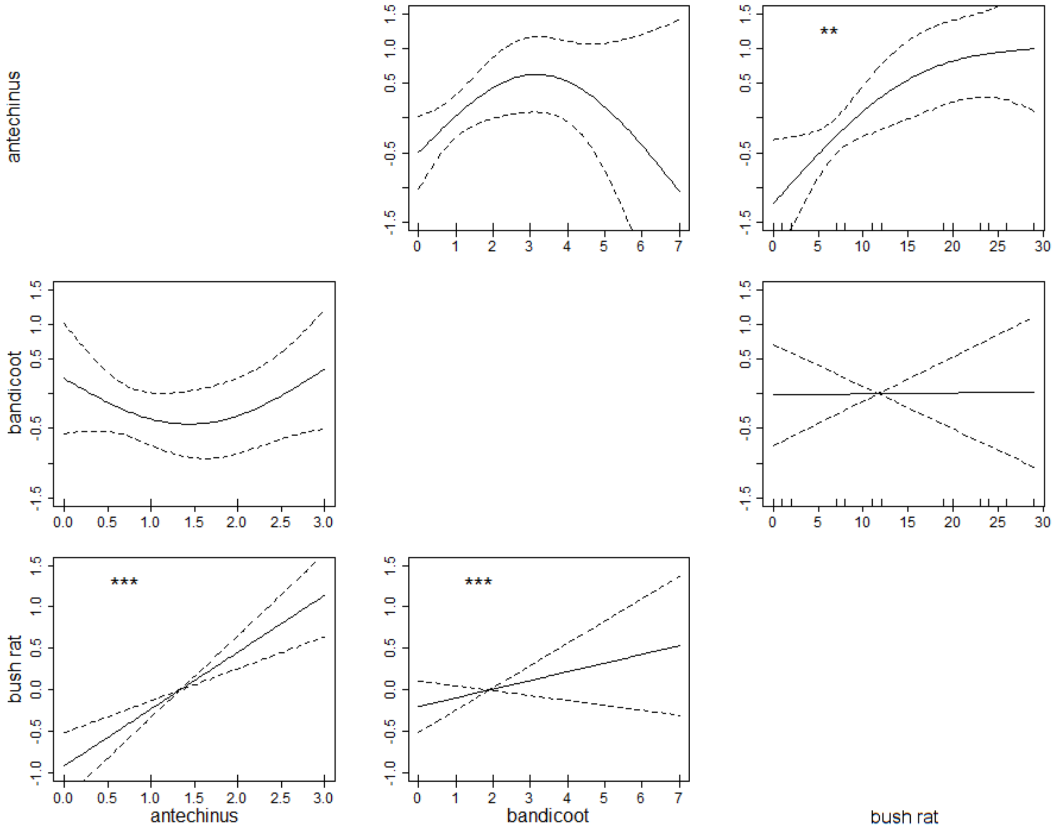


Fig. 2.9 Generalised additive mixed model (GAMM) plots of interaction amongst native mammals at the microhabitat scale

The plots give the estimated smoothing curves for GAM models on the abundance of individual fauna species in response to other fauna species. All GAMMs were modelled with Poisson distribution and a log link function, with site and transect as random factors. Bush rats were modelled as mean captures, the other species as mean individuals, and all are standardised to 100 trap sessions. * $p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$. Refer to Fig. 2.4 for more details on the interpretation of GAMM plots.

2.4 Discussion

This research shows that invasive non-native blackberry can act as an ecosystem engineer and create habitat that is essential for retaining populations of small native mammals in degraded ecosystems. Specifically, four small native mammal species used the alternative habitat provided by dense blackberry in novel ecosystems, and an increasing proportion of blackberry in the vegetation was a positive predictor for Simpson diversity and the abundance of two threatened species – the southern brown bandicoot and brushtail possum. We found that blackberry acted as an ecosystem engineer within novel ecosystems of the Mount Lofty Ranges by: (1) increasing the structure and density of vegetation and (2) providing habitat for native fauna where there is otherwise little or none. Further, blackberry potentially triggers a network of beneficial processes within degraded landscapes by retaining native fauna and the ecosystem services associated with them.

2.4.1 Effect on environmental characteristics

Blackberry contributed to the structure and density of native vegetation, although the strength of this effect varied. Vegetation was significantly denser in blackberry than in the surrounding native vegetation at hybrid and novel blackberry sites. The main difference between these hybrid and blackberry sites was the density of native vegetation along the drainage lines. Hybrid sites had retained native vegetation that contributed most of the vegetation richness and density, while the drainage lines of novel blackberry sites were mainly dominated by non-native grass with scattered native species that had been smothered by dense blackberry. This supports the view that competition does not necessarily lead to extinction (Sax et al. 2007); although blackberry had invaded the hybrid drainage lines it had not out-competed the native flora during the three years of the fieldwork component of this study. Native vegetation has likewise proven to be partially resilient to invasion by another thicket-forming species, lantana (*Lantana camara L.*) in southeastern Australia, where floristic richness remained stable below 75% lantana cover and then declined rapidly above this threshold (Gooden et al. 2009). At our novel sites, blackberry had created a thicket up to two metres high that was as dense as the native vegetation sites. These thickets increased the structural complexity in what was otherwise highly degraded, open vegetation. Similarly, McDonald and Luck (2013) found that non-native buffel grass (*Cenchrus ciliaris L.*) increased the structure and density of groundcover in semi-arid grasslands of Australia, and tended to dominate more open areas of short-lived native tussock grass and forbs. Blackberry therefore acts as an ecosystem engineer by significantly increasing the overall structure and density of the vegetation within the highly modified novel ecosystems (Jones et al. 2010).

2.4.2 Drivers of small mammal responses

Small mammal communities responded to the fragmented landscape of native vegetation and blackberry systems at different scales, highlighting the importance of multi-scale investigations and conservation strategies (Hazell et al. 2001; Fauteux et al. 2012; Meffert & Dziock 2012). Our results concur with previous studies that have identified vegetation density and complexity as the strongest positive predictor for small mammal abundance across native to highly modified novel ecosystems (Catling et al. 2002; Garden et al. 2007; Fauteux et al. 2012; Haby et al. 2012). The main positive predictors for fauna diversity and abundance were vegetation density and the proportion of blackberry within the vegetation. Small native mammals persisting in novel ecosystems were more likely to be captured in blackberry thickets, presumably because these provided the only dense habitat available. Shan et al. (2006) reported vegetation density had a significant effect on model predictions for the southern brown bandicoot in south-eastern Australia. Longland (2012) similarly found that some small native mammal species were more abundant in novel habitat created by non-native salt cedar (*Tamarix ramosissima*) than in native vegetation. While there are limited studies of mammal use of such novel habitats, other taxa have been found to use the increased structure provided by non-native engineering in novel ecosystems (eg. Castilla et al. 2004; Sogge et al. 2008; Pethiyagoda & Manamendra-Arachchi 2012; McDonald & Luck 2013). Across all sites and transects small native mammals only persisted within the blackberry-dominated drainage lines of these novel blackberry sites, with virtually no captures of any small mammals 100 m away in the surrounding native vegetation. Overall, blackberry provided habitat that retained small mammal communities in fragmented landscapes, as it was the only dense habitat available at the microhabitat scale within the novel ecosystems.

These findings are further supported by apparent interspecific interactions between the small mammal species, which revealed synchronized habitat preferences and population dynamics across the disturbance spectrum. Interspecific interactions within assemblages are often expressed via direct interference, indirect and direct competition, and predation, but communities may also be synchronized to varying degrees depending on resource availability (Liesenjohann et al. 2011; Stange et al. 2011). Antechinus and bush rats overlap in their resource needs, as they both require habitat with dense understorey and abundant arthropods, and are therefore potential competitors where these resources are limited (Cunningham et al. 2005). Cunningham et al. (2005) reported there was no evidence of association between bush rats, agile antechinus (*A. agilis)* and dusky antechinus (*A. swainsonii*) across different microhabitats in south-east Australian eucalypt forests. In contrast, the strongest interaction within small mammal communities of this present study was yellow-footed antechinus and bush rats positively predicting the abundance of each other at the site and microhabitat scale across all site types (Fig. 2.7 and Fig. 2.8). Huitu et al. (2004) found evidence of synchrony in small mammal communities in Finland, where vole and shrew populations appeared to be limited by predation and resource access more than by interspecific competition. Similarly, Carslake et al. (2011) found synchrony between common vole (*Microtus arvalis*) and two other sympatric small mammal species, potentially in response to shared predation pressure and environmental stochasticity, although habitat characteristics were not recorded in that study. The synchrony between yellow-footed antechinus and bush rats identified in the present study add further evidence to overlapping resource needs of these two species, suggesting they can co-exist in novel ecosystems when the habitat is extensive and of sufficient density.

Novel ecosystems are often associated with extensive habitat modification that is likely to alter ecological processes, shift historic patterns of resource availability and hence change interactions within and between species (Bull 2013). Nesting sites in tree hollows were found to be a limiting resources for arboreal marsupials in forest edges bordering the novel environment of pine plantations in eastern Australia, resulting in increased interspecific competition compared to continuous forest sites (Youngentob et al. 2012). Within our sites, bush rat abundance was strongly predicted by bandicoot abundance at both site and microhabitat scales, but not vice versa. This suggests that native vegetation of adequate density for bandicoots is also likely to be used by bush rats. The negative predictor of blackberry for bush rat abundance (Fig. 2.7 and Fig. 2.8) provides further evidence that bush rats are more vulnerable in novel ecosystems where bandicoots appear to be better able to exploit changes in resource availability. Our findings therefore indicate that interspecific competition is not the strongest predictor of the composition of small mammal communities in the Mount Lofty Ranges, despite their co-existence in the limited confines of blackberry thickets within novel ecosystems. Instead, it appears that external factors (i.e. predation and access to adequate habitat resources for foraging and shelter) limit antechinus and bush rat populations so their abundance is below thresholds where interspecific competition would be a limiting factor (Huitu et al. 2004).

Not only is blackberry acting as an ecological engineer that supports native fauna in novel ecosystems, but it may be acting as a “master builder” by creating the foundation for a secondary web of cascading ecosystem engineering in these highly degraded systems. The ecological engineering of blackberry increases the diversity and abundance of small mammals in highly degraded systems, which in turn act as ecological engineers and modify the environment further for other biota (Fleming et al. 2013). Small mammals forage in various ways that contribute to ecosystem processes of soil creation and aeration (Garkaklis et al. 2003, 2004; James et al. 2011; Eldridge et al. 2012), seed dispersal (Zhou et al. 2008), fungal spore dispersal (Claridge & May 1994; Pyare & Longland 2001; Vernes & Dunn 2009; Katarzyte & Kutorga 2011; Schickmann et al. 2012) and/or germination (Murphy et al. 2005; James et al. 2010). In some circumstances, mammals modify their habitat as mutually beneficial partners, as documented for the mutualistic relationships in the United States between endangered kangaroo rats (*Dipodomys ingens*) and early successional non-native plants (Schiffman 1994) and beavers (*Castor canadensis*) and aspen (*Populus tremuloides*) (McColley et al. 2012). Our findings indicate that blackberry provides conditions that promote essential ecosystem processes within novel environments by increasing vegetation complexity and retaining small mammal communities. For example, yellow-footed antechinus, bush rats, southern brown bandicoots and brushtail possums are mycophagous and disperse fungal spores (T. May, Royal Botanic Gardens Melbourne, pers. comm., 2012, T. Lebel, Royal Botanic Gardens Melbourne, pers. comm., 2012; Claridge & Barry 2000), all of these species except antechinus are frugivorous and can potentially disperse seeds (Van Dyck & Strahan 2008), and bandicoots and bush rats create digging pits and burrows (Frazer & Petit 2007; Long 2009) that improve soil properties (Fleming et al. 2013). Invasive plants like blackberry may be quite important in determining the structure and dynamics of ecological systems that have been heavily degraded. Plant species that provide vegetation structure may be essential in these systems and, if the native component is removed, an invasive species that provides similar structure could contribute directly and indirectly to maintaining essential ecosystem processes. The loss of native mammal communities, and their associated ecosystem services, may therefore have a substantial negative effect on rehabilitation of highly degraded novel ecosystems. Further research is needed to identify specifically how native mammals may act as ecosystem engineers by modifying the blackberry environment and their effect on native floral and fungal dispersal and germination. Likewise, research is necessary to explore how these ecosystem processes can be maintained whilst managing blackberry to assist natural regeneration of native plants.

2.4.3 Implications for conservation and restoration

Two opportunities for conservation and restoration within novel ecosystems are highlighted by the findings from this research: the potential to harness beneficial ecosystem processes and the importance of landscape-scale approaches where non-native habitat enables fauna populations to persist in fragmented landscapes. The findings support an integrated approach to biodiversity conservation and restoration that acknowledges non-native plants can retain and facilitate positive ecosystem processes in novel ecosystems. Managing non-native species to contain their negative impacts while enhancing their beneficial interactions also has the potential to retain native fauna assemblages that further enhance beneficial processes in healthy ecosystems (Stanley & Fowler 2004; Umetsu & Pardini 2007). It is therefore crucial to undertake biodiversity assessments, including mapping the distribution of invasive species such as blackberry, to identify both the negative and beneficial effects of invasive plants at an ecosystem and landscape level. It should then be possible to assess the likely ecosystem risks and benefits of intervention alternatives and to identify strategies that optimize the balance between beneficial enhancement and threat abatement (Sogge et al. 2008; Downey 2010). These interactions are highly complex, dynamic and vary in different contexts across the spectrum of ecosystem disturbance (Buckley et al. 2006; Seastedt et al. 2008; Hobbs et al. 2009). Restoration strategies therefore need to be gradual, anticipate change, monitor responses over time, and use adaptive management approaches across the ecosystem as a whole (Stanley & Fowler 2004; Reid et al. 2009; Paul et al. 2012; Shackelford et al. 2013).

Managing novel ecosystems requires a landscape-scale view. This approach should recognise the broader context of individual weed infestations, and the role they may play as ecosystem engineers to create habitat and landscape linkages where there are otherwise none. Our research identifies blackberry as a “master builder” that triggers a web of ecosystem engineering with the potential to facilitate mammal dispersal and gene flow between remnant patches, and support restoration of novel ecosystems by promoting native fungal and seed dispersal and germination. There may be potential to contain extensive thickets of invasive ecosystem engineers as landscape-scale buffers and linkages from novel to native ecosystems, similar to hedgerows (Michel et al. 2006; Gelling et al. 2007) and other linear habitats in Europe (Schippers et al. 2009; Ernoult et al. 2013). This could be accompanied by actively promoting regeneration of the surrounding native vegetation where it is degraded yet still present. In conclusion, our findings demonstrate that non-native ecosystem engineers can contribute to biodiversity conservation in novel systems and therefore need to be managed to enhance, rather than further degrade, ecosystem processes in fragmented landscapes.

Chapter 3 Predation risk and competition increases chronic stress in novel ecosystems

3.1 Introduction

Health condition assessments have been used since the 1970s to aid in identifying habitat suitability for wildlife populations, and have recently emerged as early warning signals for population responses to environmental change. Biologists traditionally used health indicators such as growth rates, urine biochemistry and haematology to rank habitat suitability for fish and other game wildlife (Homyack 2010). While these approaches are not commonly used in conservation, there is a growing body of research that has used physiological tools to assess habitat and inform conservation management for native biodiversity (Stevenson et al. 2005; Wikelski & Cooke 2006; Cooke & Suski 2008; Cooke & O'Connor 2010; Chown 2012; Ellis et al. 2012). A review by Homyack (2010) identified the need for research that combines a range of tools, including physiological metrics, to assess habitat quality for fauna populations. Wikelski and Cooke (2006) define this emerging discipline of conservation physiology as “the study of physiological responses of organisms to human alteration of the environment that might cause or contribute to population declines”. Physiological responses give insight into habitat quality because they translate the effect of environmental condition and change into the ecological performance of individuals and the broader population (Homan et al. 2003; Homyack 2010; Burgmeier et al. 2011; Seebacher & Franklin 2012). Incorporating physiological assessments in biodiversity conservation allows insight beyond the description of population patterns to identifying the fundamental mechanisms that cause populations to either persist or become extinct (Stevenson et al. 2005; Wikelski & Cooke 2006; Homyack 2010). Health condition can therefore act as an early warning signal for population decline by identifying physiological responses before they can be detected in fecundity and survival rates at the population level (Isaksson et al. 2005; Davis et al. 2008; Cooke & O'Connor 2010; Ellis et al. 2012). Understanding how individuals respond to their habitat at a physiological level can then be used to develop or improve predictions of population responses to different environmental conditions, including habitat modification or climate change (Homyack 2010). Cooke and O’Connor (2010) caution that further research is still needed to determine the effect of individual physiological responses on population processes for many species, and to better understand and validate the tools available within the ‘conservation physiology toolbox’.

One of the core approaches within conservation physiology is the assessment of stress levels within individuals and populations. The assessment of energetic and stress responses of organisms may aid in identifying their ability to access resources within their environment, and their ability to cope with these environmental conditions (Homyack 2010). Wikelski and Cooke (2006) define a stressor as a negative stimulus that induces a suite of physiological and behavioural stress responses as coping mechanisms. Although stress responses are essential for survival during times of acute stress in vertebrates (e.g. fight or flight response to competitor or predator attack), frequent or long-term stress (e.g. through limited access to resources) can result in delayed or reduced reproduction, increased susceptibility to disease, lower growth rates, and lower survival rates of individuals (Wikelski & Cooke 2006; Homyack 2010; Johnstone et al. 2012b). Wikelski and Cooke (2006) highlight the importance of examining not only whether individual organisms are stressed, but also the environmental conditions that stress animals at a population level, and the additive effects of these stressors for already threatened populations. For example, by combining physiological, behavioural and ecological approaches, Tracy et al. (2006) found that chronic malnourishment from limited access to critical nutrients was the cause of stress, disease and the subsequent severe declines in desert tortoise populations within native ecosystems.

Wikelski and Cooke (2006) call for quantitative models that combine physiological, behavioural and population-level demographic approaches to assess the response of organisms to human-altered ecosystems. Environments that are fragmented, degraded and/or heavily modified in other ways have the potential to increase the threat to fauna populations by exacerbating existing stressors in their natural habitat and reducing fitness levels (Cooke & O'Connor 2010; Ellis et al. 2012; Brearley et al. 2013). Evidence of heightened stress responses in modified environments is conflicting and seems to vary depending on the species and environmental context (Johnstone et al. 2012a). Hinam and Clair (2008) found that male saw-whet owls (*Aegolius acadicus*) nesting in areas with low forest cover were more stressed (based on neutrophil/lymphocyte ratio) than owls in moderate or high forest cover. They suggested the comparable stress levels between high and moderate cover may be due to increased prey availability in moderate cover. In contrast, the health condition of male oven birds (*Seiurus aurocapillus*) in continuous forest indicated high energy demands or chronic stress, although this could have resulted from defending their territory in good quality and highly competitive habitat (Mazerolle & Hobson 2002). Few studies have explored the physiological responses of mammals in modified ecosystems. Johnstone et al. (2012a) reported haematological evidence of chronic stress in agile antechinus (*Antechinus agilis*) populations living in habitat fragments compared with continuous forest populations. Similarly, faecal corticosterone concentrations of howler monkeys (*Alouatta pigra*) revealed ‘baseline’ stress levels in fragmented habitat compared to continuous habitat (Martinez-Mota et al 2007). Chronic stress was identified as potentially both a symptom and the cause of decline in howler monkey populations persisting in fragmented and degraded habitat. However, the effect of novel ecosystems and non-native plants specifically on the health condition of native fauna has not been reported. Combining physiological approaches with other traditional and emerging conservation biology approaches has the potential to predict long-term trends for the extinction risk of populations persisting in these environments.

Adrenal hormones are useful indicators of chronic stress levels of individuals. However, these indicators are very challenging to measure in free-ranging wild populations because capture stress alters the highly responsive hormone levels (Cooke & O'Connor 2010). Haematological responses have been identified as robust and reliable health indicators that are strongly linked to the adrenal stress response of wildlife populations (Davis et al. 2008). The delayed response to acute capture and handling stress detected in haematological parameters, compared with adrenal, means haematological can often provide a more reliable indication of the underlying chronic stress and disease levels (Davis et al. 2008; Maron et al. 2012; Ruykys et al. 2012). There is still much work to be done to understand the effect of environmental stressors on the haematological values of most fauna species, including many Australian mammals (Ruykys et al. 2012).

Habitat quality assessments that incorporate haematology pose their own challenges, and the most robust parameters are still being identified (Johnstone et al. 2012a). For example, white blood cell circulation is not well understood in marsupials and therefore has the potential to confound results (Davis et al. 2008; Johnstone et al. 2012a). Instead, the ratio of neutrophil to lymphocyte (N/L ratio) white blood cell types has been identified as a more reliable indicator of chronic stress for mammals (Davis et al. 2008). Eosinophils, another type of white blood cell within the immune system, can also indicate stress levels (Clark 2004). Johnstone et al. (2012a) cautioned that eosinophils were significantly higher in agile antechinus immediately after removal from traps compared with 20 min later, indicating a stress response after initial handling. While eosinophils can be a useful indicator to identify chronic stress responses in marsupials, they should therefore be used with some caution and in conjunction with other parameters.

Our focal species was the southern brown bandicoot (*Isoodon obesulus*, Shaw 1797), a medium-sized marsupial (average adult 600–900 g) that is the last remaining wild species of the Peramelidae family in South Australia (Long 2010). The meta-population in the Mount Lofty Ranges is endangered (Environment Protection and Biodiversity Conservation Act 1999, Commonwealth Government 1999) due to fox and cat predation, habitat loss and degradation (Friend et al. 2008). Although haematological reference ranges have been published for relatively few Australian fauna species (Ruykys et al. 2012), haematological reference ranges of the southern brown bandicoot have been documented for two sampling periods of a single population in Western Australia (Thomas 1990; Thomas & Bradley 1990; Wicks & Clark 2005b), and one population in Tasmania (Parsons et al. 1971). The most comprehensive reference ranges are derived from a population within 250 ha of predator-free fenced remnant woodland (Wicks &

Clark 2005a) that could be considered ‘optimum habitat’, and provide a useful comparison for the Mount Lofty Ranges meta-population. A reference range for the N/L ratio, one of the most important indicators of chronic stress, has not yet been published for this species.

Southern brown bandicoots breed throughout the year, with the peak breeding season between winter (May) and mid-summer (January) when food is most abundant (J. Packer unpublished data; Stoddart & Braithwaite 1979; Lobert & Lee 1990; Paull 1992). Adult females are thought to force their young to disperse once they are weaned so they can produce and support new litters while food resources are available (Stoddart & Braithwaite 1979). Survival is lowest during this dispersal stage and it may therefore be a time of chronic stress for bandicoot populations (Lobert & Lee 1990).

Blackberry (*Rubus anglocandicans*) is an invasive shrub that forms dense thickets that are known to provide habitat for the southern brown bandicoot within the diminishing biodiversity hotspot of the Mount Lofty Ranges in South Australia (Commonwealth of Australia 2009). This modified habitat supports higher abundance of southern brown bandicoot populations than the surrounding native ecosystems (Chapter 2), but the effect of blackberry on the population persistence of this species is unknown. We therefore investigated the influence of blackberry on health condition as an indicator of potential persistence of the southern brown bandicoot populations across sites of varying habitat quality within the Mount Lofty Ranges of South Australia. Red and white blood cell indicators of stress and condition were used to explore the interaction between habitat quality and health condition for the southern brown bandicoot and to identify:

i. how red and white blood cell values of southern brown bandicoots in the Mount Lofty Ranges compare with published reference ranges for this species

ii. whether blackberry influences red and white blood cell indicators of chronic stress for southern brown bandicoots in the Mount Lofty Ranges, and if so how.

3.2 Methods

3.2.1 Study area and sites

The health condition of the southern brown bandicoot was investigated in the Mount Lofty Ranges of South Australia (-35°E, 138°N). The region has hot, dry summers and a mean annual rainfall of 750 mm during cool winters (Wilson & Bignall 2009; Bureau of Meteorology 2012). Eleven study sites were selected within native woodland that represented three site types: dense native vegetation within continuous forest (‘native’, n = 4); dense native vegetation interspersed with blackberry (‘hybrid’ based on definition by Hobbs et al 2009; n = 3); and highly disturbed sparse native vegetation dominated by extensive blackberry (‘blackberry’ equates to novel system based on definition by Hobbs et al. 2009; n = 4). All sites were located ≥ 1 km apart for spatial independence. See Chapter 2 for more details on the study sites.

3.2.2 Animal trapping

Southern brown bandicoots were live-trapped for blood sampling over seven consecutive seasons from May 2009 (autumn) to January 2011 (summer), excluding summer 2010. Each survey site consisted of two parallel 200 m transects located approximately 30 m apart. Each transect had 10 trap stations at 20 m intervals, with one wire cage trap and one Type A Elliott trap at each station. Traps were baited with a mixture of rolled oats, peanut paste and a small amount of linseed oil. Traps were set and checked in the morning and late afternoon during summer, autumn and spring and in the morning only during winter. The number of trap nights varied from 5–7 nights to safeguard animal welfare in extreme weather conditions, and all animal work was consistent with the appropriate ethical and legal standards.

Captured bandicoots were uniquely marked at first capture with a passive integrated transponder tag inserted subcutaneously in the rump above the right hind leg (Haby et al. 2013). Morphometrics, reproductive condition, health and body condition, dental health and ecto-parasitic load of each bandicoot was recorded at their first capture of each season as part of a broader study into the effect of habitat quality on the health condition of the southern brown bandicoot (not reported here).

3.2.3 Blood sampling and measurements

Blood samples were collected from southern brown bandicoots and analysed for haematological and biochemistry parameters. The haematological results are reported here. All blood sampling was undertaken by veterinarians from Zoos South Australia (Zoos SA) and/or the School of Animal and Veterinary Science, University of Adelaide. The project provided an opportunity to develop protocols for conducting health checks and blood sampling with wild populations of the southern brown bandicoot in South Australia. The protocols presented in this section were adapted for wild populations and field surveys from those developed by Clark (Clark 2004; Wicks & Clark 2005a).

Bandicoots were only considered for blood sampling if they were > 300 g, male, or non-lactating females. Lactating females were identified by checking the teats of all females and gently squeezing any that were enlarged (> 50% larger than other teats on the same female) to see if milk was expressed (Scott et al. 1999). Blood samples were taken on site wherever possible to minimise handling time and stress to the animals. All samples were collected ≤ 24 hours from the time traps were set at the site. Each individual was clinically examined and then anaesthetised using an Ayres t piece with Isoflurane (Attane, Parmtech, Australia) within oxygen at a rate of 4–5% to induce anaesthesia, and 2–3% for maintenance. Individuals took < 1 min to become anaesthetised and remained sedated for up to 5 mins. The femoral vein was the most reliable and consistent venepuncture site, followed by the left jugular vein. Blood samples were taken with a 30-gauge needle and 1 ml syringe, and a maximum of 1.5 ml of blood was taken for each sample. Most samples were < 1 ml. Blood smear slides were made immediately from fresh blood, air dried, fixed in 100% ethanol and later stained with Diff-Quik stain set. The rest of each blood sample was divided between 1 ml tubes containing ethylene diamine tetraacetic acid (EDTA) tubes for haematological studies, and serum tubes for biochemical analyses (published separately). Individuals were observed until they recovered from anaesthesia and then released at site of capture as soon as possible.

All haematological analyses were undertaken by Brian Matthews at the Adelaide Health Clinic laboratories of Zoos SA within four hours of collection. Red blood cell (RBC; x10^{12} cells per litre) and white blood cell (WBC; x10^{9} cells per litre) counts, haemoglobin (Hb), haematocrit (Hct), mean cell volume (MCV), mean corpuscular haemoglobin (MCH), mean corpuscular haemoglobin concentration (MCHC) and platelets were estimated for each sample on an automated Beckman Coulter T890 (Ruykys et al. 2012). Further analysis of reticulocytes was conducted on a Beckman Coulter Unicell DXH 800.

White blood cell composition and morphology, nucleated red blood cells, red blood cell polychromatophils and Howell-Jolly bodies, were calculated from blood film slides under light microscopy (Olympus BH2) with 400x magnification (Johnstone et al. 2012a). Absolute values and the proportion of white blood cells that were neutrophils, lymphocytes, monocytes, eosinophils, basophils and annular leukocytes were estimated for each slide. These differential white blood cell counts were conducted as an indication of chronic stress levels in the sampled bandicoots. Counts were estimated with visual sweeps longitudinally along the stained blood slide (n = 100 cells; Johnstone et al. 2012a). We used the absolute values from cell counts to compare chronic stress levels between site types and seasons, and to model the effect of habitat on chronic stress. Absolute values for each cell type are independent of total white blood cell counts, and are recommended for comparative analysis over proportional values (% WBC; Clark 2004). We estimated and report % counts in addition to absolute values of white blood cells for two reasons: % is sometimes the only value reported, including in older studies of southern brown bandicoot haematological (Parsons et al. 1971; Thomas 1990), and because N/L ratio is a useful indicator of chronic stress that can be estimated from % values for neutrophils and lymphocytes. Absolute and % values are therefore reported to enable comparison with other haematological studies of the southern brown bandicoot (Parsons et al. 1971; Thomas 1990; Thomas & Bradley 1990; Wicks & Clark 2005a).

Four white blood cell parameters were modelled to examine the effect of specific habitat characteristics on the health condition of the southern brown bandicoot: neutrophils, lymphocytes; N/L ratio; and eosinophils. These parameters are regarded as four of the most robust and reliable haematological indicators of chronic stress for mammals (Clark 2004; Davis et al. 2008; Johnstone et al. 2012a). One red blood cell parameter, polychromatophils, was modelled to identify whether the significant variability we detected between site types during exploratory data analysis was influenced by particular habitat characteristics.

3.2.4 Habitat assessment

Vegetation characteristics were recorded for each site in November 2010 as explanatory variables to assess the effect of habitat characteristics on the health condition of the southern brown bandicoot. Variables were measured by allocating trapping transects into twenty 10 x 10 m plots and randomly selecting five along one transect. Plots at blackberry sites were positioned 1 m within the blackberry thicket to minimise any edge effect. All vascular plant species within the plot were recorded, along with the number of individuals for native species that are known or potential food and/or shelter resources for the endangered southern brown bandicoot. Point-intercepts surveys were conducted

Table 3.1 Description of vegetation characteristics surveyed as explanatory variables at sites containing southern brown bandicoots

Values for all variables are based on pooled means across 5 randomly selected 10x10m plots per site. Variables in bold were retained in the models, all others were excluded due to collinearity.

	explanatory habitat variables
VEG	vegetation community
	native plant richness - mean no. of native plant species
	exotic plant richness - mean no. of exotic plant species
	vegetation density – mean pole touches 0 - 1.5 m
	vegetation density – mean pole touches 0 - 50 cm
	vegetation density – mean pole touches 50 cm – 1 m
	vegetation density – mean pole touches 1 - 1.5 m
BB	**pole touches by blackberry as % of veg density 0 - 1.5 m**
	blackberry area (m^2)
DBH	**mean diameter at breast height (cm) for trees >10 cm**
	canopy height (m)
	canopy % cover
	stags – mean no. individuals >10cm DBH
EWD	**mean pole touches of elevated woody debris (1-10cm diam) detached and trapped in vegetation**
	logs – mean no. >10 cm DBH and >1 m long
litter	**mean litter depth (mm)**
moisture	**soil moisture index (1 - 8) measured with soil probe**
	soil pH measured with soil probe
slope	degrees measured with inclinometer
aspect	N, S, E, W measured with compass
structure	number of vegetation strata with > 10 pole touches
xanth	*Xanthorrhoea semiplana* density – mean no. individuals

with a levy pole at ten randomly selected points within each plot. We used a 2 metre levy pole (1 cm diameter) divided into 25 cm increments and recorded the total number of touches (up to maximum of 10) for each plant species at each increment. Further measurement details for each explanatory habitat variable are given in Table 3.1.

3.2.5 Statistical analysis

A mixed modelling approach was used to explore the effect of habitat characteristics on the health condition of southern brown bandicoots. Additional blood samples were taken, but these were excluded if individuals presented as unhealthy during clinical examination e.g. major lice infestations or obvious wounds, or the haematological values indicated potential health issues without clinical signs e.g. if two or more haematological values were outside the published reference range (Wicks & Clark 2005a).

Exploratory data analysis was conducted to check for normality, outliers, collinearity and relationships. Other outliers were not excluded based on the recommendations of Solberg (1987). We calculated descriptive statistics for 12 red blood cell and 14 white blood cell parameters from the Mount Lofty samples. As red and white blood cell values were determined with different methods, we dealt with these separately. We were able to compare the range, mean and standard deviation for 16 of these parameters with reference values for the southern brown bandicoot (Wicks & Clark 2005a; see also Parsons et al. 1971; Clark 2004).

All haematological values were tested for normality with the Shapiro-Wilk normality test, and were transformed with natural log where appropriate. We tested for differences between site types to examine how the health condition of southern brown bandicoots captured in different densities of blackberry compared with those in native ecosystems. If absolute values were normal, either as raw data or once transformed, we generated generalised linear mixed models (GLMMs) with Poisson distribution and log link function for the haematological variable as response and site type as explanatory fixed effect. Year and season were combined into an additional explanatory variable (year*season) to account for any systematic spatio-temporal variances resulting from repeated observations from the same site over different seasons (Cunningham et al. 2005; S. Delean pers. comm.; Zuur et al. 2009). We therefore included site, year and year*season as random factors in these models to test for differences between site types. If data were non-normally distributed and not transformable, we used Kruskal-Wallis one-way ANOVA with post-hoc Wilcoxon rank sum test to test for differences between site types. We repeated this approach to test for difference between seasons for each haematological parameter.

Further analysis was conducted to explore whether habitat variables influenced the chronic stress responses of southern brown bandicoots in the Mount Lofty Ranges. Our response variables were neutrophils, lymphocytes, N/L ratio, eosinophils and polychromatophils. We selected five explanatory variables of habitat condition from our initial set of 18 explanatory variables: vegetation density (VEG); blackberry density as a proportion of overall vegetation density (BB); tree abundance (DBH); elevated woody debris (EWD); and litter depth. This final set was selected on the basis of lowest Pearson correlation coefficient (<0.60), lowest variance inflation factors (< 3.00; Zuur et al. 2009) and strongest prediction of southern brown bandicoot abundance (Chapter 2). Generalised linear mixed models were used to explore the relationships between habitat and haematological responses as preliminary analyses identified linear relationships between the response and explanatory variables (Zuur et al. 2009; Zuur et al. 2012). We generated GLMMs with Poisson distribution and logarithmic link functions for each of the five haematological responses because the data were derived from absolute counts of each cell type and the mean of each parameter was <5 (Bolker et al. 2009). The GLMMs used site, season and year*season as random effects to account for expected variability within sites and seasons. Models were compared and ranked based on % deviance (% DEV) (Brook et al. 2006). The deviance of the null model (intercept as fixed effect and site, season and year*season as random effects) was calculated and used to obtain the percentage of deviance explained by GLMMs for each response (Brook et al. 2006; Sodhi et al. 2008). All models with % deviance > 5 were considered to adequately explain the model deviance and provide reliable predictions for the response (Sodhi et al. 2008). Model fit was also assessed by calculating R^2 for GLMMs using the technique developed by Nakagawa and Schielzeth (2013).

All analyses were conducted in the R statistical package v.3.0.0 (R Core Team 2013) using the *stats* package v.2.15.2 for Shapiro-Wilk and Kruskal-Wallis tests , *lme4* package v.0.999999.2 for GLMMs (Bates et al. 2013), *multcomp* package v.1.2.18 for Tukey's Honestly Significant Difference tests (Hothorn et al. 2008), and *MuMIn* package v.1.9.5 (Bartoń 2013) for model ranking.

3.3 Results

A total of 129 blood samples were collected from 79 individual southern brown bandicoots (male = 44, female = 35) across 11 sites representing a continuum of human-altered habitats from native to hybrid and novel ecosystems. Here we provide the first account of haematological values for marsupial populations persisting in novel systems, and hence also the first comparison of haematological-derived health condition between native and novel habitats for this group.

3.3.1 Neutrophil / lymphocyte ratio

Reference ranges for N/L ratios have not previously been published for the southern brown bandicoot. N/L ratio ranged from 0.11 to 3.18 in our samples (n=124), with a mean of 1.0 (Table 3.2). Similarly, reference values for platelets have not previously been published for this species. Parsons et al. (1971) recorded platelet levels in the southern brown bandicoot as “normal” but did not report actual numbers. The absolute levels of platelets in our samples (n=96) ranged from 157–801 10^9/L with a mean of 357 x 10^9/L.

3.3.2 Comparison with reference ranges

We calculated range and means for 26 haematological parameters, and compared 16 of these with reference ranges for the southern brown bandicoot (Parsons et al. 1971; Wicks & Clark 2005a). The Mount Lofty samples were more variable than the reference ranges, with all but one of the standard deviations greater than those of the reference ranges (Table 3.2). Live-trapping is known to influence acute stress for red squirrels (*Tamiasciurus hudsonicus*; Bosson et al. 2012), brushtail possums (*Trichosurus vulpecula*; Buddle et al. 1992) and agile antechinus (Johnstone et al. 2012a). To check whether the variability detected in the Mount Lofty samples was exacerbated by the length of time in capture, we calculated means for 124 samples collected ≤12 hours from trap set (Table 3.3). There were no significant differences in mean values of samples taken ≤12 hours compared with ≤24 hours after traps were set. Thomas (1990) has reported significant variation in southern brown bandicoot haematological values previously. Likewise, Packer (1968) reported significant variations in red and white blood cell values in quokka (*Setonix brachyurus*). Further, the standard errors for our samples indicated that variability was within the expected ranges of each parameter.

The mean values from our samples for all parameters were within the published reference ranges (Table 3.2). However interestingly, nearly half the measures had ranges and mean that were considerably different from the reference values. Red blood cell parameters tended to be lower than the reference ranges, and white blood cell values higher (Table 3.3). For example, the percentage of circulating red blood cells identified as polychromatophils in our samples ranged from 0–12.25%, considerably higher than the 0–4.4% reported by (Wicks & Clark 2005a). In terms

Table 3.2 Summary of red and white blood cell values in southern brown bandicoot, Mt Lofty Ranges of South Australia

Abbreviations for parameters are given in the text. Haematological values are based on 129 samples from 79 individuals (male = 44, female = 35) across 11 sites. Reference ranges provided from Wicks & Clark (2005) are minimum–maximum (mean).

	n	min	max	mean	SE	SD	Wicks & Clark (2005)
red blood cells							
red blood cells (RBC; x10^{12}/L)	107	4.66	8.28	6.46	0.06	0.62	5.42-8.40 (6.96)
haemoglobin (g/L)	107	101	163	129	1.21	12.53	120-167 *(145)*
haematocrit (L/L)	107	0.28	0.50	0.39	0.00	0.04	0.32-0.51 (0.43)
MCV (fL)	107	50.90	67.40	60.48	0.32	3.34	57.1-65.8 (61.4)
MCH (pg)	107	16.70	23.40	20.05	0.13	1.32	19.1-23.4 (20.8)
MCHC (g/L)	107	295	368	332	1.73	17.92	318-364 (338)
platelets (x10^{9}/L)	96	157	801	367	14.97	146.66	
polychromatophils (% circulating RB(	107	0.00	12.25	2.05	0.24	2.51	0.0-4.4 (0.8)
nucleated RBC (x10^{9}/L)	107	0.00	0.68	0.05	0.01	0.10	
nucleated RBC (per 100 WBC)	107	0.00	12.00	0.86	0.17	1.75	0.0-7.5 (0.8)
Howell-Jolly bodies (% mature RBC)	107	0.00	0.23	0.05	0.00	0.05	0.0-1.0 (0.1)
reticulocytes (% circulating RBC)	24	1.32	18.88	6.00	0.80	3.94	
white blood cells							
white blood cells (WBC; x10^{9}/L)	124	1.50	11.90	6.02	0.20	2.21	1.25-7.68 (3.5)
neutrophil (x10^{9}/L)	124	0.26	5.94	2.41	0.10	1.17	0.32-3.97 (1.34)
neutrophil (% WBC)	124	9.00	70.00	40.32	1.18	13.17	
lymphocytes (x10^{9}/L)	124	0.77	7.81	2.91	0.14	1.52	0.34-5.68 (1.74)
lymphocytes (% WBC)	124	19.00	83.00	47.74	1.32	14.75	
neutrophil : lymphocyte ratio	124	0.11	3.18	1.03	0.06	0.67	
monocytes (x10^{9}/L)	124	0.03	0.71	0.18	0.01	0.13	0.00-0.38 (0.04)
monocytes (% WBC)	124	1.00	9.00	3.03	0.16	1.75	
eosinophils (x10^{9}/L)	124	0.00	1.10	0.27	0.02	0.21	0.00-0.91 (0.31)
eosinophils (%)	124	0.00	15.00	4.53	0.31	3.44	
basophils (x10^{9}/L)	124	0.00	0.11	0.02	0.00	0.03	0.00-0.05 (0.01)
basophils (%)	124	0.00	2.00	0.27	0.04	0.48	
annular WBC (x10^{9}/L)	124	0.00	0.78	0.20	0.01	0.15	0.00-0.33 (0.07)
annular WBC (% circulating WBC)	124	0.00	15.00	3.40	0.20	2.27	

Table 3.3 Differences between means of ≤ 12hr, ≤ 24 hr and reference ranges for haematological parameters measured in the southern brown bandicoot

Bold indicates mean values below the reference range of (Wicks & Clark 2005a), while ***italics*** indicates the means were above the reference range.

	≤ 12 hr mean	**≤ 24 hr mean**
red blood cells	*n=79*	*n=107*
red blood cells (RBC; x10^{12} /L)	**6.35**	6.46
haemoglobin (g/L)	**127**	129
haematocrit (L/L)	**0.38**	0.39
MCV (fL)	**60.03**	60.48
MCH (pg)	20.14	**20.05**
MCHC (g/L)	336	**332.00**
polychromatophils (% circulating RBC)		2.05
nucleated RBC (per 100 WBC)		0.86
Howell-Jolly bodies (% mature RBC)		0.05
white blood cells	*n=96*	*n=124*
white blood cells (WBC; x10^{9} /L)	5.83	***6.02***
neutrophils (x10^{9} /L)	2.35	***2.41***
lymphocytes (x10^{9} /L)	2.82	***2.91***
monocytes (x10^{9} /L)	0.17	***0.18***
eosinophils (x10^{9} /L)	0.25	**0.27**
basophils (x10^{9} /L)	0.01	0.02
annular WBC (x10^{9} /L)	***0.21***	0.2

of white blood cell parameters, the absolute number of neutrophils (x10^9/L) ranged from 0.26–5.94 (mean 2.41) in our samples and 0.32–3.97 (1.34) in the reference range. Lymphocytes (x10^9/L) ranged from 0.77–7.81 (2.91) compared with 0.34–5.68 (1.74) in the reference ranges. The absolute number of eosinophils (x10^9/L) ranged from 0–1.10 (0.27) in our samples compared to 0–0.91 (0.31) in the Wicks and Clark (2005a) reference range.

3.3.3 Effect of habitat on health condition

Bandicoots exhibited similar haematological values across all sites. Only one parameter, the proportion of red blood cells that were polychromatophils, was significantly different between site types. Polychromatophils are immature red blood cells and increased levels can indicate chronic stress in fauna populations (Clark 2004). Hybrid and blackberry sites had significantly higher polychromatophils than native sites (Kruskal Wallis: $P = 0.003$; Fig. 3.1).

Elevated woody debris and blackberry density were identified as predictors for the polychromatophil differences across site types. Polychromatophils were negatively influenced by elevated woody debris (GLMM top-ranked models: % deviance = 5.95, Table 3.4; GLMM individual estimates $z = -2.03$, $P = 0.04$; Table 3.5), which corresponded with the significantly lower polychromatophils at native sites. Conversely, blackberry was a weak positive predictor individually for polychromatophils (GLMM: % deviance = 3.52; GLMM $z = 1.61$, $P = 0.11$), with the highest levels at blackberry-dominated sites. No other habitat characteristic had a significant effect on health condition.

3.3.4 Effect of season on health condition

Samples were collected across seven consecutive seasons, excluding summer 2010. There were no significant haematological differences detected between the seasons (Fig. 3.2). However, autumn (March–May) was a strong negative predictor for eosinophils (GLMM $z = -4.46$, $P = <0.001$; Table 3.5) and a negative predictor for N/L ratio (GLMM $z = -2.45$, $P = 0.01$).

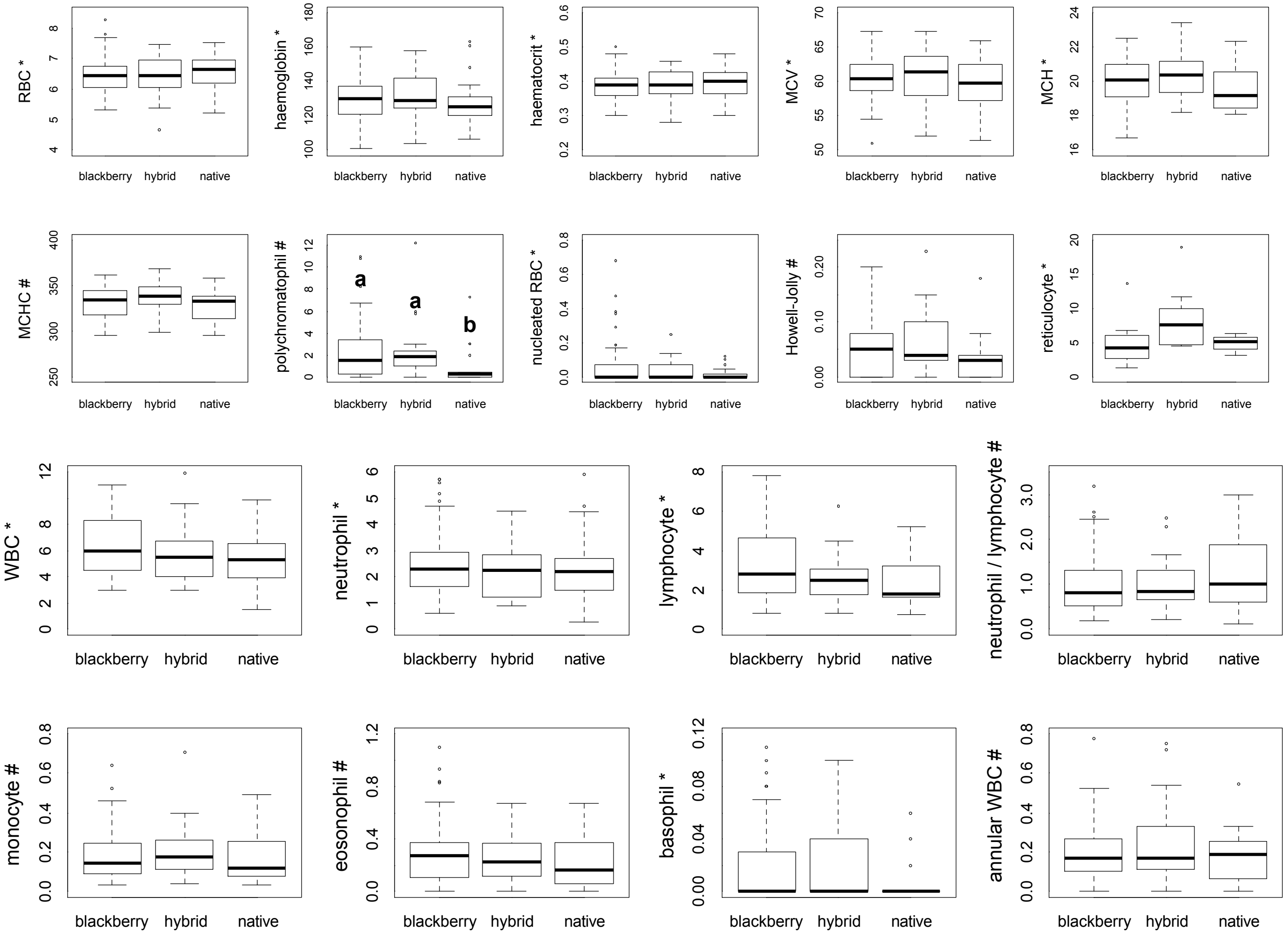


Fig. 3.1 Comparison of mean haematological values for southern brown bandicoots across site types

Differences between site types were tested with generalised linear mixed models (GLMMs) and post-hoc Tukey's Honestly Significant Difference (*) or Kruskall-Wallis with post-hoc Wilcoxon rank (#). Each haematological parameter was tested as the absolute value and as natural log transformed. Sample sizes for red blood cell parameters across the three site type were: blackberry (n = 67); hybrid (n = 20); and native (n = 20). Sample sizes for white blood cell parameters were: blackberry (n = 78); hybrid (n = 26); and native (n = 20). Different letters indicate statistically significant differences, and were only detected for polychromatophils.

Table 3.4 Top ranked generalised linear mixed models (GLMMs) for haematological parameters in the southern brown bandicoot

Full GLMMs were generated with Poisson distribution and log link functions from the absolute counts for each haematological parameter. The global model included season, blackberry, veg density, DBH, EWD, and litter as explanatory variables and site, season, and year by season as random factors. Only the strongest models with $\Delta < 2.00$ are presented.

rank	*model*	*edf*	*-LL*	*AICc*	Δ *AICc*	*% DEV*	$R^2_{GLMM (m)}$
neutrophils : lymphocytes							
1	NULL	4	-8.728	25.792	0.00	0.00	0.00
2	BB	5	-8.199	26.907	1.11	6.07	0.01
3	veg	5	-8.631	27.771	1.98	1.15	0.00
neutrophils$^{\pi}$							
1	NULL	4	-6.102	20.54	0.00	0.00	0.00
lymphocytes$^{\pi}$							
1	NULL	4	-6.567	21.471	0.00	0.00	0.00
2	BB	5	-6.023	22.554	1.08	8.23	0.01
eosinophils							
1	NULL	4	-7.499	23.334	0.00	0.00	0.00
2	BB	5	-7.074	24.656	1.32	5.67	0.03
3	veg	5	-7.167	24.843	1.51	4.47	0.03
polychromatophils							
1	EWD	5	-32.91	76.404	0.00	5.95	0.06
2	BB + EWD	6	-32.4	77.646	1.24	7.37	0.08
3	BB	5	-33.76	78.105	1.70	3.52	0.04
4	BB + litter	6	-32.73	78.295	1.89	6.46	0.08
5	NULL	4	-34.98	78.361	1.96	0.00	0.00

Table 3.5 Haematological estimates for southern brown bandicoots calculated individually using generalised linear mixed models (GLMMs)

Individual GLMMs were generated with Poisson distribution and log link functions from the absolute counts for each haematological parameter. Site, season, and year by season were modelled as random factors. Only the strongest models with $\Delta < 2.00$ are presented.

	neutrophils : lymphocytes					**neutrophils**				**lymphocytes**				**eosinophils**					**polychromatophils**				
	estimate	*SE*	*z*	*P*		*estimate*	*SE*	*z*	*P*	*estimate*	*SE*	*z*	*P*	*estimate*	*SE*	*z*	*P*		*estimate*	*SE*	*z*	*P*	
season - autumn	-0.51	0.21	-2.45	0.01	*	0.10	0.15	0.64	0.52	0.26	0.14	1.86	0.06	-1.65	0.37	-4.46	<0.001	***	0.02	0.18	0.11	0.91	
veg density	0.00	0.00	0.44	0.66		0.00	0.00	-0.08	0.94	0.00	0.00	-0.61	0.54	0.00	0.00	-0.81	0.42		0.00	0.00	0.40	0.69	
BB density	-0.48	0.47	-1.02	0.31		-0.02	0.35	-0.05	0.96	0.35	0.33	1.04	0.30	0.74	0.80	0.92	0.36		0.69	0.43	1.61	0.11	
DBH	0.00	0.00	0.25	0.80		0.00	0.00	-0.37	0.71	0.00	0.00	-0.70	0.48	0.00	0.00	-0.36	0.72		0.00	0.00	-0.74	0.46	
EWD	0.00	0.02	0.13	0.90		0.00	0.01	-0.08	0.93	0.00	0.01	-0.03	0.98	-0.01	0.03	-0.23	0.82		-0.04	0.02	-2.03	0.04	*
litter	0.03	0.09	0.30	0.76		0.02	0.07	0.30	0.77	-0.01	0.06	-0.12	0.91	-0.06	0.15	-0.38	0.71		0.12	0.10	1.23	0.22	

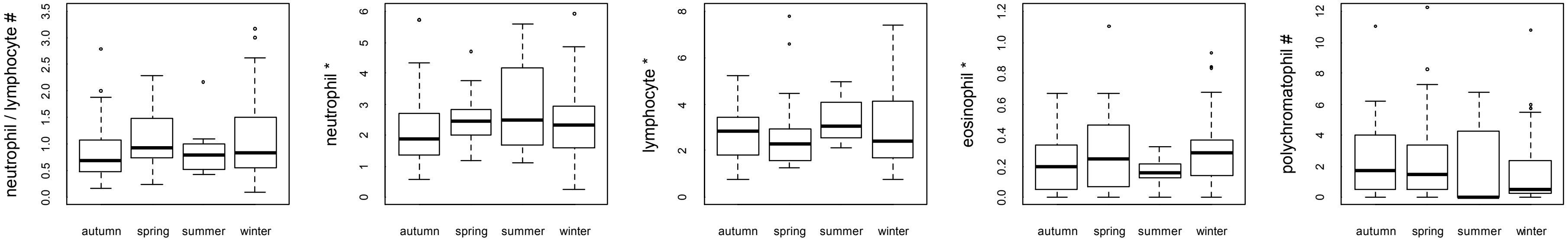


Fig. 3.2 Comparison of mean haematological values for southern brown bandicoots across seasons

Differences between site types were tested with generalised linear mixed models (GLMMs) and post-hoc Tukey's Honestly Significant Difference (*) or Kruskall-Wallis with post-hoc Wilcoxon rank (#). Each haematological parameter was tested as the absolute value and as natural log transformed. Sample sizes for red blood cell parameters across the seasons were: summer (n = 7); autumn (n = 30); winter (n = 55); and spring (n = 15). Sample sizes for white blood cell parameters were: summer (n = 7); autumn (n = 38); winter (n = 59); and spring (n = 20). No significant differences were detected.

3.4 Discussion

Our research partially supports the view that physiological measures can detect environmental stressors for fauna populations before they manifest in population density or reproductive trends. We found that human-altered ecosystems may be significantly more stressful environments for the southern brown bandicoot than native woodland remnants. Further, comparison with reference ranges revealed evidence of chronic stress in the meta-population persisting in the fragmented landscape of southeastern Australia compared with predator-free woodland in southwestern Australia (Wicks & Clark 2005a). This research highlights the importance of multi-scale physiological investigations, as detection may only be possible at a fine scale within a population, across the meta-population at landscape scale, or by comparing physiological indices with published values for other populations.

3.4.1 Site scale: territorial stress in human-altered habitat

Disturbed ecosystems appear to be more stressful environments than native woodland for the southern brown bandicoot. The raised polychromatophil levels found here at hybrid and blackberry sites indicate higher levels of chronic stress than at the native sites. Polychromatophils, one indicator of chronic stress, were negatively predicted by elevated woody debris (native sites) and weakly positively predicted by increasing proportions of blackberry within native vegetation. There are three possible explanations for this trend: (1) acute stress related to capture myopathy; (2) assessor bias; and (3) environmental stress.

Extreme stress from capture and handling can cause capture myopathy, a potentially fatal disorder in wild populations of native fauna that is due to physiological overload from acute stress (McMahon et al. 2013). Spleen contraction can be associated with capture myopathy and is a condition where the spleen contracts suddenly and expels immature red blood cells, and can therefore result in unnaturally high levels of polychromatophils (B. Matthews, Zoos SA, pers. comm. with P. Clark). To the best of our knowledge, this phenomenon has not yet been documented in any species. This potential spleen effect is unlikely to explain the significant differences and GLMM predictions for polychromatophils detected in our samples because the differences were strongly correlated with site types.

The second potential explanation for raised polychromatophils at blackberry sites is that they are the result of observer bias. Red blood cells are recorded as polychromatophils when they are bluer than expected within the normal range of mature red blood cells (Clark 2004; B. Matthews, pers. obs.). A subjective margin of error is therefore possible where one assessor may record cells as polychromatophils, while another may make a professional judgement they are mature red blood cells. This issue is particularly problematic if more than one observer is involved in the estimation process. All haematological analyses were conducted by a single observer in the present study, so site-specific differences cannot be explained by observer bias.

The final possible explanation for significant polychromatic differences between site types is that human-altered habitats are more stressful for bandicoots than native ecosystems. There are few physiological studies that assess the direct effect of human-altered habitats on native fauna persistence. However, Brearley et al. (2012) found that forest edges adjacent to major roads were stressful environments for squirrel gliders (*Petaurus norfolcensis*) in southeast Queensland, based on the physiological indicator of hair cortisol levels. In contrast, patch interiors were the least stressful habitat for gliders. Our findings followed a similar pattern, with bandicoots in native habitats showing signs of decreased stress levels compared to increased stress-related polychromatophils in blackberry sites. Considering these native sites had the lowest bandicoot abundance, chronic stress may be competition-related. Multiple indicators suggest that blackberry sites have the highest bandicoot abundance (Fig. 2.4, Chapter 2); greatest availability of food resources (Table 4.2, Chapter 4); and are acting as source populations for the region (Table 4.5, Chapter 4). Further, microhabitat assessments revealed that the matrix surrounding blackberry within novel sites is inhospitable for small native mammals (Fig. 2.5, Chapter 2). Blackberry thickets are therefore likely to be highly sought-after habitat. Bandicoots in blackberry sites had considerably higher levels of tail loss, body scars and ear injuries than either hybrid or native sites (J. Packer, unpublished data). Thomas (1990) used body scarring as an indicator of intraspecific aggression, confirming that the high levels of injury we observed in blackberry systems are likely to be competition-related. With such a high level of territorial competition, bandicoots are likely to experience heightened levels of chronic stress in these environments.

Heightened stress during autumn, as indicated again by changes in blood chemistry, may also be the result of increased competitive pressure during the peak dispersal period. Autumn is the period of greatest juvenile dispersal in the Mount Lofty Ranges (J. Packer, unpublished data) and is therefore likely to be a time of many territorial disputes. Thomas (1990) found that fighting was greatest between male bandicoots and was heightened during April–June (autumn–winter). Low eosinophils during autumn could therefore be linked to chronic stress, potentially from heightened stress as autumn is the season of highest population density and dispersal. Chronic stress in quokka (*Setonix brachyurus*) was found to be heightened seasonally during times of greatest population density (Packer 1968). The seasonal effect of juveniles and heightened competition for resources associated with their dispersal could be causing heightened stress responses in autumn. Further evidence of seasonal stress is given by Kitaysky et al. (2006), who found that declining juvenile recruitment in red-legged kittiwake seabirds (*Rissa brevirostris*) was linked to the seasonal stress of learning to capture prey at sites where food resources were limited and patchy. If seasonal competition was driving the high levels of polychromatophils at blackberry sites, season effects would identify autumn in the top-ranked and/or individual GLMMs. This was not the case, so it seems that the novel habitat of blackberry itself is more stressful. One final question remains: if high polychromatophils in blackberry is due to competitive-related chronic stress, why isn't this chronic stress evident in other haematological parameters? Further research is required to tease out the effects of competition versus habitat on raised polychromatophils in novel ecosystems.

3.4.2 Landscape scale: reduced health condition in a fragmented system

Our findings revealed considerable and widespread differences in the haematological values of samples from woodlands in the Mount Lofty Ranges compared with reference ranges derived from apparently optimum habitat of remnant and predator-free woodland in southwestern Australia. All except one of our haematological parameters were either above or below the reference ranges. Bandicoots sampled for the reference ranges were sedated with Zoletil50 (Virbac, Peakhurst, NSW; Wicks & Clark 2005a), whereas we sedated with isoflurane (as per some samples in Wicks & Clark 2005a). Wicks and Clark (2005b) noted that no comparison has been made of the effect of different anaesthetics on haematological parameters, but that similar effects have been reported for both dissociative and volatile anaesthetics. Anaesthetics are therefore unlikely to account for the differences in haematological levels detected between the reference ranges and our samples. Despite extensive literature searches in Web of Knowledge and Google Scholar, it was not possible to identify any published studies on the effect of physical injuries on the haematological profile of native fauna from captive or wild populations. Clinical advice was therefore sought from wildlife veterinarian specialists, who confirmed the haematological values observed in our samples indicate chronic low grade disease and increased levels of injury compared to the reference ranges (D. McLelland, Zoos SA, pers. comm.).

Differences in food resources have been found to induce chronic stress and result in population declines in seabirds (Kitaysky et al. 2006). Arthropods are known to be the primary food resource for southern brown bandicoots throughout the year (Quin 1985; Mallick et al. 1998; Keiper & Johnson 2004), supplemented by plant material and truffle fungi (Keiper & Johnson 2004). We found significantly higher biomass of arthropods in blackberry (Table 4.2, Chapter 4), suggesting that food resources do not drive chronic stress levels at a site scale in this region. However, the reduced arthropod diversity at blackberry sites and limited truffle samples overall may provide a lower quality habitat, and more nutritionally stressful environment, than woodland in Western Australia (Wicks & Clark 2005a).

Predation pressure may also be responsible for the differences detected between our samples and the reference ranges. Bandicoots sampled by Wicks and Clark (2005a) were from a fenced predator-free population in native woodland. In comparison, the Mount Lofty Ranges is a peri-urban environment where red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) populations are present without any control programs. These introduced predators are known to be one of the major threatening processes for the southern brown bandicoot, particularly in highly fragmented and degraded habitats such as the Mount Lofty Ranges (Friend et al. 2008). The peri-urban landscape of southeast Queensland has similarly been reported as stressful for squirrel gliders, particularly along roadside edges where there are few protected denning hollows (Brearley et al. 2012). Based on two indicators of potential predation, we found that predation risk was consistently lower across native sites. Foraging by southern brown bandicoots during Giving Up Density (GUD) trials demonstrated heightened predation risk at the blackberry sites away from blackberry thickets, and consistently lower predation risk at native sites (Chapter 4). Fox scat abundance was positively correlated with southern brown bandicoot abundance across 13 sites in the Mount Lofty Ranges (GLM $P < 0.001$; J. Packer, unpublished data). Bandicoots are therefore likely to be more chronically stressed by predation risk at the blackberry sites than at the native sites. Similarly, Johnstone et al. (2012a) found agile antechinus persisting in forest fragments appeared to be experiencing higher levels of chronic physiological stress. However, considering hybrid drainage lines provided significantly denser habitat than any other vegetation type in the study area (Chapter 2), chronic stress does not appear to be linked solely to vegetation density and protection from predators. Further research is therefore required to identify the range of factors that may be increasing the stress levels, and associated extinction risk, of southern brown bandicoots in fragmented landscapes.

3.4.3 Conservation physiology as an early warning signal

Chronic physiological stress and disease in wildlife populations has the potential to reduce fecundity, increase mortality and ultimately lead to population declines (Brearley et al. 2012; Johnstone et al. 2012a; Maron et al. 2012; Brearley et al. 2013). This link is particularly strong in novel landscapes that have been dramatically altered by human intervention (Isaksson et al. 2005; Hedblom & Soderstrom 2012). Understanding these physiological processes has the potential to complement more traditional pattern–process assessments of fauna persistence, and physiological approaches are therefore being increasingly used within conservation management (Davis et al. 2008; Brearley et al. 2013). Our research provides further evidence that environmental stressors resulting from human-induced landscape change can trigger complex responses that increase chronic stress, competition-related injury and disease levels in native fauna populations. In conclusion, we found that southern brown bandicoots within novel blackberry-dominated ecosystems demonstrated higher levels of chronic stress and competition-related injury than bandicoots within native ecosystems in the Mount Lofty Ranges and Western Australia. Additionally, haematological profiles associated with chronic stress and disease may be an early warning sign of extinction risk in southern brown bandicoots persisting in the fragmented 'canary landscape' of the Mount Lofty Ranges.

Chapter 4 Non-native blackberry (*Rubus anglocandicans*) increases habitat quality and recruitment for native mammals

4.1 Introduction

Biological invasions are a major threat to native ecosystems globally, yet in some landscapes they can also play a positive role in facilitating the persistence of native species (Rodriguez 2006). Rodriguez (2006; see also Crooks 2002; Martin & Murray 2011; Schlaepfer et al. 2011; Ortega et al. 2006) predicted invasive species are most likely to facilitate native species if they provide critical resources, replace the functional role of a native species, increase the complexity of habitat, limit competition and/or reduce predation. Non-native ecological engineers that 'create' habitat where it is otherwise lacking are the most likely to have a positive effect and increase the diversity and abundance of native fauna (Chapter 2; Wright & Gribben 2008). However, little is known of the net effect of these non-native engineers on the population productivity and persistence of native fauna.

Fauna populations require access to high quality habitat to persist in an ecosystem long-'term. Any habitat that supports a source population with reproductive success greater than mortality can be defined as 'high quality habitat' for fauna populations (Van Horne 1983; Christopherson & Morrison 2004; Pulliam 1988; Pulliam & Danielson 1991). Since habitat use/availability does not guarantee the persistence of populations by itself, species abundance and density may not be reliable indicators of habitat quality (Van Horne 1983; Hobbs & Hanley 1990; Vickery et al. 2011). Native fauna populations in decline can be described as persisting in either 'sinks' (Pulliam 1988) or ecological traps ('attractive sinks'; Kristan 2003; Battin 2004). Habitat use and abundance can sometimes disguise negative population trends. For example, Wright and Gribben (2008) found that high abundance of *Anandara trapezia* cockles within invasive seaweed habitat did not match cockle fitness, and was therefore masking low quality habitat and a potential extinction debt. Reduced cockle fitness in a novel habitat provides further evidence of non-native species acting as population sinks; but could the opposite be true in novel habitats where non-native plants support fauna communities that would otherwise be locally extinct (Chapter 2)? Or are novel habitats merely delaying extinction debts and supporting population sinks? Quantifying the net effect of invasive plants at a population-level is therefore essential to assess whether novel habitat acts as a population sink, source or ecological trap for native fauna (Battin 2004; Severns 2011; Harabiš & Dolný 2012). Only then can critical novel habitat be identified and strategies developed to balance the conservation needs of native fauna with targeted management.

Individual fitness measures that quantify success during a breeding season (e.g. young per female per season) provide important insight into habitat quality for individuals at a fine scale (Nilsen et al. 2004), but may reveal little about the potential for a particular habitat to support long-term persistence of populations (Pidgeon et al. 2006). Population fitness, and more recently productivity, have therefore been identified as more reliable indicators of habitat quality for fauna populations than individual measures or population density (Pidgeon et al. 2006; Chalfoun & Martin 2007; Mosser et al. 2009). Indicators of population fitness, including the number of young produced, juvenile survival and recruitment into the population (Lin & Batzli 2001; Pidgeon et al. 2006; Chalfoun & Martin 2007; Mosser et al. 2009), are calculated across the survey population. Although productivity reflects individual and population fitness, it is assessed with a spatial focus (e.g. number of young produced per unit area) and gives an indication of the carrying capacity of particular habitats (Mosser et al. 2009). High quality habitats are therefore expected to have high levels of reproductive success and productivity.

Assessing the net benefit of native fauna–invasive plant interactions therefore requires intensive research that moves beyond diversity and abundance to assessing impacts on fitness and population productivity of native fauna (Sogge et al. 2008; Wright & Gribben 2008). A few studies have examined the effect of invasive species on fitness and productivity for native birds (Ortega et al. 2006; Sogge et al. 2008) and marine fauna (Byers et al. 2010; Cebrian et al. 2012), or described the interference of invasive plants in the nesting success of reptiles and amphibians (see review by Martin & Murray 2011). However, the potential for invasive species to provide high quality habitat for fauna is unknown (Wright & Gribben 2008). We are aware of only two previous studies on the effect of invasive species on habitat quality for native mammals. Ellis et al. (1997) found that the reproductive parameters indicating condition in white-footed mice (*Peromyscus leucopus*) were comparable between invasive *Tamarix* and native cottonweed habitats based on adult sex ratios and the percentage of adult males and females that were breeding. Invasive starthistle (*Centaurea solstitialis*) can also provide comparable habitat quality to surrounding non-native grassland for native rodents, based on the percentage of adults breeding in populations (Christopherson & Morrison 2004). To the best of our knowledge, this present study is the first to investigate the impact of an invasive plant on the individual fitness, recruitment and net productivity of native mammal populations and, in particular, the impact on a threatened marsupial species.

Blackberry (*Rubus anglocandicans*) is an invasive shrub that acts as an ecological engineer in novel ecosystems (Chapter 2). This species is the most widespread European blackberry in Australia and has formed dense thickets along many waterways and drainage lines in the Mount Lofty Ranges of South Australia (Evans & Weber 2003; Government of South Australia 2010; NSW Department of Primary Industries 2010). The southern brown bandicoot (*Isoodon obesulus*) is a small marsupial that is endemic to Australia and the last remaining species of the Peramelidae family in South Australia. The sub-species *Isoodon obesulus obesulus* occurs in highly fragmented populations in southeastern Australia and is nationally endangered (Environment Protection and Biodiversity Conservation (EPBC) Act 1999, Commonwealth Government 1999) due to introduced predators (particularly foxes and cats) and habitat loss resulting from altered fire regimes, native vegetation clearance and modification (Friend et al. 2008). This sub-species was listed under the EPBC Act (Commonwealth Government 1999) due to "a severe reduction in numbers" across its current range compared to its historic distribution (Fig. 4.1).

Previous research has found that blackberry can retain diverse small mammal communities in novel ecosystems, including increased abundances of the southern brown bandicoot (Chapter 2). However, the effect of blackberry on habitat use and population persistence for any taxa is unknown. The framework of invasive species as potential facilitators for native biodiversity (Rodriguez 2006) provides a useful approach to examine how blackberry is impacting on the southern brown bandicoot. We investigated the influence of blackberry density on population density, fitness and productivity as indicators of habitat quality for bandicoot populations within remnant native vegetation through to novel ecosystems within the Mount Lofty Ranges of South Australia. Three critical questions were examined:

i. how do resources (such as food and protective cover) associated with different densities of blackberry compare with that of remnant native ecosystems?

ii. what is the influence of blackberry on indicators of population persistence for the southern brown bandicoot; specifically the density of adult females, individual fitness (percentage of females breeding and pouch young per litter), and population productivity (juvenile recruitment)?

iii. if blackberry contributes to population persistence for the southern brown bandicoot in novel ecosystems, how is it facilitating this effect?

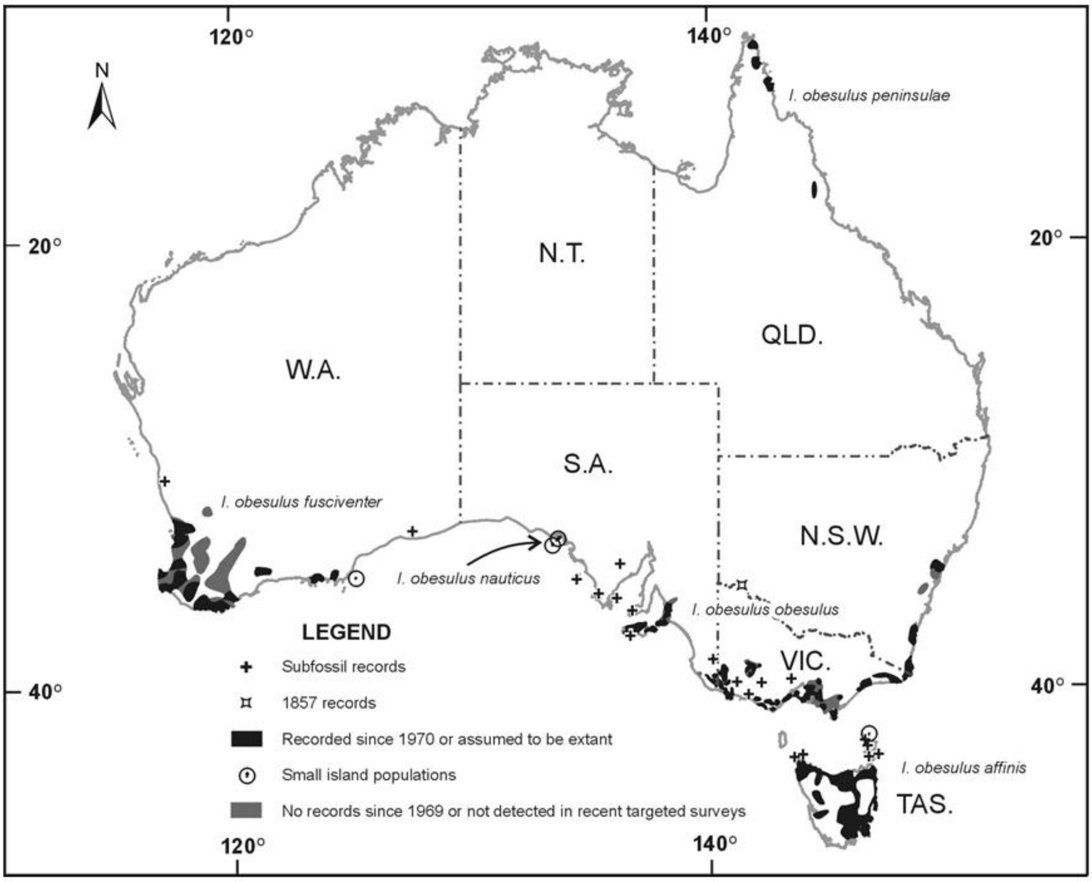


Fig. 4.1 Distribution of the southern brown bandicoot (*Isoodon obesulus*) in Australia

The map shows the historic and current distribution of the southern brown bandicoot as it is currently recognised (Source: Paull et al. 2013).

4.2 Methods

4.2.1 Study area

This study was conducted in the Mount Lofty Ranges of South Australia (-35°E, 138°N), a National Biodiversity Hotspot that has only 8% of native vegetation remaining within a peri-urban human population (Commonwealth of Australia 2009). The study area was located within 7,500 ha of the Ranges that represent human-modified landscape states that vary from fragmented through to relictual in different parts (McIntyre & Hobbs 1999). Remnant patches were dominated by *Eucalyptus* woodland associations and formed a mosaic with agriculture, semi-rural properties and peri-urban residential areas (Fig. 4.2; Paton et al. 2004; Government of South Australia 2008). The area has a mean annual rainfall of 750 mm with cool, wet winters and hot, dry summers (Wilson & Bignall 2009; Bureau of Meteorology 2012).

Potential study sites were identified by the presence of fresh diggings or other recent records of the southern brown bandicoot. Eight sites were selected for this study from thirteen sites surveyed for the small mammal investigation (Chapter 2) because they had the highest bandicoot abundance for each of three site types. These site types represented a disturbance continuum: from relatively dense native vegetation within continuous forest/woodland that had minimal recent disturbance and nil or few blackberry plants (‘native’, n = 2); to dense native vegetation that had been moderately disturbed and was interspersed with blackberry (‘hybrid’ based on definition by Hobbs et al 2009; n = 3); and highly disturbed sparse native vegetation dominated by extensive blackberry (‘blackberry’ ”novel system” in Hobbs et al. 2009; n = 3). The native sites were regarded as some of the highest quality habitat for bandicoots in the region (Paull 1992; K Abley pers. comm.; Sanderson & Kraehenbuehl 2006). Additional native sites were surveyed as part of the broader study, but are not included here because State Government authorities disallowed pitfall and truffle surveys due to the presence of *Phytophthora cinnamomi,* a highly invasive soil-borne mould, and the extreme risk of spreading it through soil disturbance. All sites were located in drainage lines and all blackberry thickets were at least 200 m long.

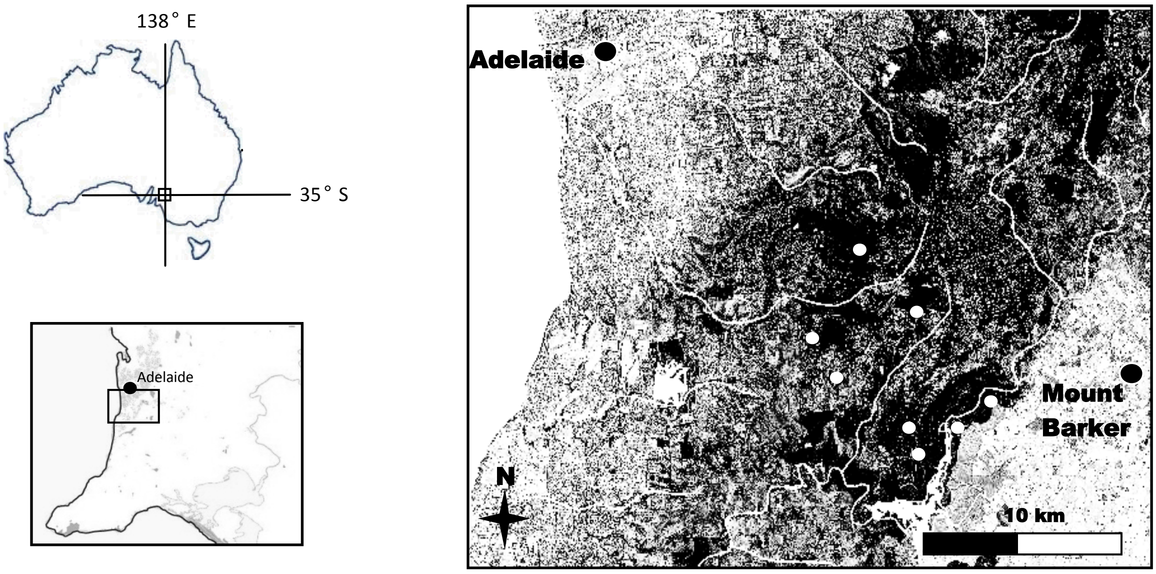


Fig. 4.2 Map of the eight study sites within the Mount Lofty Ranges of South Australia surveyed for the southern brown bandicoot

Only 8% of remnant vegetation remains as relatively intact yet isolated patches. The study sites are shown as white circles, major waterbodies as white lines, and remnant native vegetation as large dark grey areas. Smaller areas of dark grey are remnant or introduced canopy, mostly with little or no understorey.

4.2.2 Study population

Southern brown bandicoots were trapped for 11 consecutive seasons, from June 2008 to January 2011, within the central Mount Lofty Ranges meta-population (Bentley 2010). Captured individuals were uniquely and permanently marked with a passive integrated transponder tag inserted subcutaneously in the rump above the right hind leg (Haby et al. 2013). Unique ear notches were also given as a secondary individual identification.

We used four demographic measures to assess habitat quality for southern brown bandicoot populations: density (number of adult females known to be alive), individual fitness (percentage of adult females breeding and number of pouch young per litter) and population productivity (number of independent juveniles recruited into the population). Adult females are considered to represent the future breeding capability of fauna populations (Stoddart & Braithwaite 1979; Ballinger & Congdon 1981; Mosser et al. 2009), and litter size has previously been used in southern brown bandicoots as an index of fitness (Dexter et al. 2011). We therefore surveyed the density, fitness and reproductive output of females as indicators of population persistence. Female bandicoots were recorded as adults when ≥ 400 g which corresponds with pes length approximately 50 mm (Lobert & Lee 1990 Table 1 gives weight and pes including claw; see also Mallick et al. 1998).

Breeding activity varies across the range of southern brown bandicoots, with populations in south-eastern Australia breeding all year and others seasonally with peaks in food abundance (Lobert & Lee 1990; Long 2010). Although the Mount Lofty meta-population has a seasonal breeding season with most litters produced from June to December (Paull 1992), breeding has been recorded throughout the year (Paull 1992; Kovac 2002; Sanderson & Kraehenbuehl 2006). Breeding females were defined as either carrying pouch young or having one or more large lactating teats (Mallick et al. 1998; Scott et al. 1999). Enlarged teats (> 50% larger than other teats on the same female) were gently squeezed and the female was recorded as lactating if milk was expressed (Scott et al. 1999). Teats started to visibly contract two or more days after lactation ceased (J. Packer pers. obs.). The number of pouch young per litter was determined by counting the number of young in the pouch, or the number of enlarged lactating teats indicating the number of young that were suckling but not captured with the female (Heinsohn 1966; Lobert & Lee 1990; Mallick et al. 1998; Scott et al. 1999). For example, Heinsohn (1966) observed that young southern brown bandicoots spend time in a nest before being weaned, and Duffy and Rose (2007) reported juveniles consume milk and solid food during this period. Lobert and Lee (1990) cautioned that counts of enlarged teats are only estimates of litter size, as newborn *Isoodon macrourus* have been observed attached to teats that are enlarged from a prior litter, and young could suckle from multiple teats. Neither situation has been reported for the southern brown bandicoot, nor was it observed in the present study. To further reduce the risk of miscalculating litter sizes, we only counted enlarged teats as an indicator of litter size if the teats were lactating. Litter size has been linked to female body mass in the rufous spiny bandicoot (*Echymipera rufescens australis),* and litter frequency and size to rainfall and arthropod availability in the southern brown bandicoot (Lobert & Lee 1990; Shevill & Johnson 2008). Litter size was therefore assumed to be a reliable indicator of habitat quality, with larger litters indicating higher quality habitat.

The young of southern brown bandicoots become independent and disperse soon after being weaned (Heinsohn 1966; Lobert & Lee 1990). Juvenile bandicoots weigh an average of 105–140 g when they are weaned (Lobert & Lee 1990; Duffy & Rose 2007). We therefore classified juvenile bandicoots as dependent and pre-dispersal young when < 140 g, and as independent dispersing juveniles when ≥ 140 g and < 400 g for females or < 500 g for males (Heinsohn 1966; Lobert & Lee 1990; Dufty 1994; Todd et al. 2001; Duffy & Rose 2007). Independent juveniles were classified as transients if they were only captured in one season, or as recruits if they were captured for two or more seasons (Lobert & Lee 1990). New individuals trapped in the first or last season were not included in the recruitment data as it was not clear whether they were recruits or transients (Dexter et al. 2011). Previous research suggests adult southern brown bandicoot females may force their young to disperse in order to retain access to resources for producing new litters (Stoddart & Braithwaite 1979). This strategy of high reproductive output and high dispersal presumably enables the southern brown bandicoot to respond rapidly when resources are plentiful within unpredictable and patchy ecosystems. However, the loss of individuals is highest during the dispersal phase of juveniles, with as few as 12% recruited (Stoddart & Braithwaite 1979; Lobert & Lee 1990). Juvenile survival is therefore one of the primary determinants of population growth, and recruitment may be a useful indicator of population productivity and persistence in the southern brown bandicoot.

4.2.3 Habitat characteristics

Vegetation characteristics were surveyed in October 2010 at five plots along each drainage line. Plots were identified by dividing trapping transects into twenty 10 x 10 m plots and selecting five based on computer-generated random plot numbers. A range of parameters were used to assess vegetation complexity and density (Table 4.1) as indicators of potential shelter available. Data were averaged across the five plots. We conducted vegetation surveys as part of a broader investigation into the influence of blackberry on native fauna across a disturbance continuum.

Table 4.1 Description of vegetation and food resource characteristics surveyed at each site

All variables are based on pooled means across 5 randomly selected 10 x 10 m plots per site. Variables in bold were retained in the models, all others were excluded due to collinearity.

	explanatory habitat variables
vegetation	
VEG	vegetation community
	native plant richness - mean no. of native plant species
	exotic plant richness - mean no. of exotic plant species
	vegetation density – mean pole touches 0 - 1.5 m
	vegetation density – mean pole touches 0 - 50 cm
	vegetation density – mean pole touches 50 cm – 1 m
	vegetation density – mean pole touches 1 - 1.5 m
BB	**pole touches by blackberry as % of veg density 0 - 1.5 m**
DBH	**mean diameter at breast height (cm) for trees >10 cm**
	canopy height (m)
	canopy % cover
	stags – mean no. individuals >10cm DBH
EWD	**mean pole touches of elevated woody debris (1-10cm diam) detached and trapped in vegetation**
	logs – mean no. >10 cm DBH and >1 m long
litter	mean litter depth (mm)
structure	number of vegetation strata with > 10 pole touches
xanth	*Xanthorrhoea semiplana* density – mean no. individuals
food	
arthropod	**arthropod abundance - no. individuals per site per season**
	arthropod Simpson diversity per site per season
	arthropod biomass 2-5 mm - no. individuals x 2 mm
	arthropod biomass 6-10 mm - no. individuals x 6 mm
	arthropod biomass 11-15 mm - no. individuals x 11 mm
	arthropod biomass >15 mm - no. individuals x 15 mm
truffle fungi	truffle abundance - no. samples per site per season
	truffle Simpson diversity per site per season

from native to hybrid and novel ecosystems. Further details of these surveys are outlined in Chapter 2. Availability of potential food resources was assessed by surveying two of the major food sources for bandicoots: arthropods and hypogeous fungi (Quin 1988; Lobert & Lee 1990; Keiper & Johnson 2004). Previous studies have confirmed these two food groups comprise the majority of southern brown bandicoot diet: Broughton & Dickman (1991) found arthropods comprised 78% of bandicoot diet in south-western Western Australia, and more recently Keiper and Johnson (2004) identified invertebrates as the major food item (35–56% of faecal samples) across all seasons on Cape York, followed by roots (7–27%) and hypogeous fungi (0–26% seasonally, hereafter referred to as "truffles"). Pitfall and truffle surveys were therefore conducted for four consecutive seasons from March 2010 to January 2011. One trapping station was selected per site and season with computer-generated random numbers. Truffle surveys were conducted at stations based on the technique developed by Claridge et al. (2000). Plots commenced at the trap station, with the first of five 20 m x 10 m plots located within the drainage line (data presented here) and additional plots 0–10 m, 10–20 m, 20–30 m and 30–40 m away. Truffles were surveyed using a garden rake with four prongs to scrape away the leaf litter and soil to a maximum depth of 100 mm. Initial trials were conducted to identify the amount of time required to collect the majority of truffle genera able to be detected within the plot. A similar method of time-adjusted surveying was used by Paull (2003) to account for significant differences in vegetation density when searching for bandicoot diggings. Based on the findings from this trial, plots were surveyed for 20 minutes each in native vegetation and 30 minutes in blackberry due to the extra time required to move around the plot. All truffle genera were identified from macro- and microscopic characters and were confirmed by a mycologist, Pam Catcheside (pers. comm., SA Herbarium; Trappe & Castellano 1991 ; Fuhrer 2005; Abell 2011). All genera were included as there is currently no knowledge of southern brown bandicoot preference for particular truffle genera.

Dry pitfall traps were installed at alternate trapping stations (10 per site) to capture arthropods. Pitfalls were 150 x 150 mm plastic tubs with a 90 mm hole cut in the centre of the lid to prevent escapees. To prevent pitfalls from becoming water-logged, drainage holes were drilled in the bottom of the tub then covered by mesh, and a second tub with open drainage holes installed below the first. All tubs were installed so the lid was level with the ground surface, and soil was smoothed around the hole. Pitfalls were left *in situ* (with a plastic plug inserted to minimise disturbance when opening and closing the pits), and were opened for one week each season. Pitfalls were checked daily during the weeks they were open, and any skinks or large predatory arthropods were recorded and released. All samples were stored in 70% ethanol. Arthropods were sorted and identified to order based on Jennings (2003a); (Jennings 2003b) and Tilling (1986). The full set of data was then used to select the six arthropod orders that contribute most to southern brown bandicoot diet (Heinsohn 1966; Opie 1980; Lobert 1985; Quin 1985; Mallick et al. 1998; Keiper & Johnson 2004). Arthropod richness, Simpson diversity and abundance (based on order) were calculated from this subset of six orders. Biomass was calculated across the four size classes of 2–5 mm, 6–10 mm, 11–15 mm and >15 mm by multiplying the number of samples by the minimum size in that class (Paull et al. 2011).

Giving Up Density (GUD) experimental trials were conducted to assess the predation risk perceived by southern brown bandicoots in native vegetation compared to blackberry thickets. GUD trials can give an indication of protective cover and potential shelter resources available in different systems, and have previously been used to assess habitat quality for small mammals (Olsson et al. 2002; Vickery et al. 2011; Arthur et al. 2012). We ran trials across the three site types for seven nights during the new moon phase, and excluded the first two nights to account for the time it took for animals to locate, explore and forage from the feed trays with some consistency (i.e. data based on five nights; Yunger et al. 2002; Kotler et al. 2010). Two hybrid and two blackberry sites were surveyed once each. We surveyed two locations 100 m apart in one remnant forest patch (native site) as the risk of infection from *Phytophthora cinnamomi* prevented surveys being conducted at other native sites, and we did not detect any bandicoot activity in other drainage lines within the patch. Concurrent trapping surveys revealed minimal movement of bandicoots between the two drainage line locations, with only a single male being trapped in both, suggesting the locations were likely to be visited by different individuals. Three paired GUD stations were set up at each site, with one station in the drainage line (1 m within the blackberry thicket at hybrid and blackberry sites) and one station 5 m away on the edge of the drainage line. Trays were baited with live mealworms, a favoured food source for wild bandicoots when they are provided as supplementary food (Paull et al. 2011). Preliminary GUD trials were conducted during March 2011 to identify the number of mealworms required per station to ensure some remained after bandicoots foraged as an indication of the upper GUD threshold. Bandicoots ate all mealworms that were hidden within a single tray of sand during these trials. We therefore developed a system of two trays with 12 tubs each per GUD station to make the mealworms harder to detect. Tubs were pre-drilled with drainage holes, secured to the tray with cable ties and filled with coarse damp sand. One tray provided a ‘low density’ of 15 live mealworms, with five in each of three randomly selected tubs, while the other tray provided a ‘high density’ of 40 mealworms distributed across eight randomly selected tubs. Digital infrared cameras (Moultrie Game Spy I–40) were used to confirm that mealworms were consumed predominantly by bandicoots, and to record behaviour associated with foraging in the different vegetation densities (data not presented here). Cameras were set to take 30 seconds of video and one still photograph, with a trigger delay of at least one minute between images.

4.2.4 Statistical analyses

We used a mixed modelling approach (Wood 2006; Zuur et al. 2009) to investigate the persistence of southern brown bandicoots in response to blackberry and other habitat characteristics at an individual and population level. Five explanatory habitat variables that were used in previous studies (Chapters 2 and 3) were retained for modelling of reproductive responses. Exploratory data analysis was conducted to check for outliers, collinearity and interrelationships. Litter was the least significant explanatory variable for reproductive responses, and models were unnecessarily complex and would not converge when it was included. Based on the principle of parsimony, choosing the simplest modelling approach possible, litter was therefore excluded for this investigation of bandicoot persistence (Crawley 2013).

The four vegetation variables were checked against truffle and arthropod measures for collinearity using Pearson correlation coefficients (<0.60) and variance inflation factors (<2.00; Zuur et al. 2009; Zuur et al. 2012). Arthropod abundance was retained to allow a diverse set of explanatory variables with no collinearity and ecological diversity. The final set of five explanatory variables was therefore: vegetation density, blackberry as % of vegetation density, DBH, elevated woody debris and arthropod abundance. This final set of explanatory variables fell within the recommended ratio > 10 records per parameter (Wintle et al. 2005; Zuur et al. 2012).

We tested for differences in explanatory habitat resources and bandicoot responses using generalized linear mixed models (GLMMs) with post-hoc Tukey's Honestly Significant Difference (HSD) multiple comparison tests. GLMMs with site type as the explanatory variable were generated, with Poisson distribution and log link function for each response variable that was count-derived (vegetation density, elevated woody debris, pouch young per litter, female density, and recruitment), and GLMMs with Gaussian distribution and identity link function for the remaining response variables. Southern brown bandicoot data were based on four seasons, and standardized to 100 trap sessions for each site and season. Year and season were combined into an additional explanatory variable (year*season) to account for any systematic spatio-temporal variances resulting from repeated observations from the same site over the eleven seasons (Cunningham et al. 2005; S. Delean pers. comm.). We included site, year, and year*season as random factors to test for differences in bandicoot responses between site types. All GLMMs were tested for significance with Tukey's HSD.

We investigated the explanatory habitat variables responsible for the differences between site types using generalized additive mixed models (GAMMs). We used GAMMs within an information-theoretic framework to explore the complex relationships and ecological thresholds between bandicoot populations and their habitats. GAMMs have the flexibility to model non-linear responses and thresholds, and to further account for potentially systematic spatio-temporal variances from repeated sampling over sites and seasons (Cunningham et al. 2005; Jensen et al. 2005; Zuur et al. 2009). GAMMs also addressed the zero-inflated and count-derived nature of our mark-recapture data, particularly at the native sites where bandicoot density and reproductive success was low. GAM models were generated with Laplace approximation to explore the predictive power of environmental variables on the four reproductive measures: proportion of females breeding, pouch young per litter, female density and juvenile recruitment. GAMMs were generated with Gaussian distribution and identity link function for the proportion of females breeding, and with Poisson distribution and log link function for the other three response variables. Site, season, and year*season were included as random factors to remove the variability effect of repeated measures from the same site over the eleven seasons. Full GAM global models with all explanatory variables for each reproductive response were generated in MuMIn (Bartoń 2013), and then all of the potential variable combinations were tested and ranked using the *dredge* function in MuMIn. We assessed the GAMM rankings according to their weightings derived from Akaike's information criteria for small sample size (AICc; Burnham & Anderson 2002; Zuur et al. 2009). All strong models with $\Delta \leq 2$ are reported. We also generated GAMMs for each explanatory habitat variable against each bandicoot response to examine the predictive power of each combination individually. Goodness-of-fit was assessed for each individual GAMM based on deviance explained (R^2), and models with $R^2 > 0.05$ were considered to adequately explain the model deviance and provide reliable predictions for the response (Sodhi et al. 2008). *P* values were also calculated for each individual GAMM, and all *P* values reported are from these models unless stated otherwise. Smoothed terms were considered to be statistically significant when their *P* values were <0.05 and R^2 was > 0.05. We then plotted these individual GAMMs to identify any non-linear relationships and significant thresholds between habitat characteristics and bandicoot reproductive responses.

All analyses were conducted in the R statistical package version 3.0.0 (R Core Team 2013). GLMMs were generated using the extension package *lme4* version 0.999999.2 (Bates et al. 2013) and assessed with Tukey's Honestly Significant Difference (HSD) tests in the *multcomp* package version 1.2.17 (Hothorn et al. 2008). GAMMs were developed in *gamm4* version 0.1.6 (Wood 2012), then assessed and ranked with the *MuMIn* package version 1.9.5 (Bartoń 2013).

4.3 Results

4.3.1 Habitat differences

Hybrid sites had the densest vegetation (x̄ = 325.33 vegetation touches per plot) and hence provided significantly more protective habitat for small mammals than either native (x̄ = 216.00) or novel blackberry sites (x̄ = 245.32, Tukey HSD *P* <0.001; Table 4.2). The dense vegetation of these hybrid sites was mainly comprised of native *Lepidosperma* and *Gahnia* tussocks, scattered large trees (x̄ = 82.67 cm DBH) and live blackberry (x̄ = 13% of total vegetation density). In contrast, vegetation at the novel blackberry sites was predominantly live blackberry (x̄ = 49% of 245.32 overall vegetation touches) combined with dead blackberry canes as elevated woody debris (EWD x̄ = 9.45). Native sites were not significantly different to these novel sites in terms of vegetation density (x̄ = 216.00, HSD *P* = 0.104) or complexity, with comparable EWD (x̄ = 14.5, HSD P = 0.270), tree abundance (x̄ = 60.00, HSD *P* = 0.189) and litter (x̄ = 2.36, HSD *P* = 0.220).

Food resources varied significantly across site types, with an overall trend of higher truffle diversity and availability at native sites and more abundant arthropods at blackberry sites (Table 4.2). Six genera of truffles were identified: *Amarrendia, Chamonixia, Descomyces, Hydnoplicata, Hysterangium*, and *Mesophellia* (Table 4.3). All six genera were detected at the native sites, two at hybrid sites (*Chamonixia* and *Descomyces*) and two at the blackberry sites (*Amarrendia* and *Hysterangium*). Truffle diversity and abundance was therefore significantly higher at native sites (diversity x̄ = 3.15; abundance x̄ = 9.50 samples per site and season) than either hybrid (diversity x̄ = 0.67, HSD *P* <0.001; abundance x̄ = 1.33, HSD *P* <0.001) or blackberry sites (diversity x̄ = 0.68; abundance x̄ = 1.97). Truffle diversity and abundance were excluded from the modelling process because the low detection rates gave very low predictive power for the GAMMs.

We identified 14 orders of arthropods, including five of the six orders that have been identified as major prey items for the southern brown bandicoot: *Araneae* (spiders), *Coleoptera* (beetle larvae and adults), *Haplotaxida* (earthworms), *Isopoda* (slaters) and *Lepidoptera* (butterfly or moth larvae; Table 4.4; Heinsohn 1966; Opie 1980; Lobert 1985; Quin 1985; Mallick et al. 1998; Keiper & Johnson 2004). *Orthoptera* (crickets) have also been identified as common prey items for bandicoots (Heinsohn 1966; Mallick et al. 1998), but were not captured in the pitfall traps. Native sites had significantly higher diversity of arthropods (x̄ = 4.08; Table 4.2) compared to hybrid (x̄ = 3.13, HSD *P* <0.001) and blackberry sites (x̄ = 3.13, HSD *P* <0.001). However, the overall arthropod abundance was significantly higher at blackberry sites (x̄ = 25.88) compared to native sites (x̄ = 10.79, HSD *P* <0.001). The most significant differences in arthropod biomass were that blackberry sites had many more small arthropods (2–5mm $\bar{x}$ = 4.70; 6–10mm $\bar{x}$ = 86.93) compared to native sites (2–5mm $\bar{x}$ = 0.91; 6–10mm $\bar{x}$ = 28.27). Arthropod diversity was excluded from models due to collinearity with the five habitat variables (Zuur et al. 2009), leaving arthropod abundance as the explanatory variable retained as an indication of food availability across the site types. This approach is consistent with previous dietary studies of the southern brown bandicoot that have used invertebrate abundance as an estimate of food availability (Broughton & Dickman 1991; Mallick et al. 1998).

The GUD trials revealed significant differences in the way southern brown bandicoots perceived the different microhabitats available within their environment. Perceived predation risk was lowest in the drainage lines of hybrid sites ($\bar{x}$ = 1.08 mealworms left per tray), with significantly fewer mealworms remaining in these trays compared to 5 m away in the native vegetation ($\bar{x}$ = 13.75, HSD *P* <0.001; Fig. 4.3). Blackberry thickets in the drainage lines of novel blackberry sites also provided significantly more protection for bandicoots ($\bar{x}$ = 5.27) than the surrounding vegetation ($\bar{x}$ = 23.18, HSD *P* <0.001). Vegetation density was not significantly different across the native sites (Chapter 2), and this was reflected in the similar foraging rates of bandicoots in the native drainage lines ($\bar{x}$ = 3.56) compared with 5 m away ($\bar{x}$ =3.51, HSD *P* = 1.000). Drainage lines at both hybrid and blackberry sites provided similar levels of protective cover, and hence perceived predation risk, as the number of mealworms remaining at these sites were comparable to the native sites. Remote camera images supported these findings, with more visits to the trays by bandicoots than either yellow-footed antechinus (*Antechinus flavipes*) or bush rats (*Rattus flavipes*), the other small mammal species present locally.

Table 4.2 Differences between habitat resources across site types

The total number of replicates per site type is stated. Replicates within each site were pooled and averaged, with five replicates for vegetation, four for truffles and ten for arthropod surveys. Arthropod and truffle data were also pooled and averaged across the four seasons. Means and standard distribution (SE) are based on data that were further pooled and averaged for each site type. Arthropods are based on the six orders that have previously been reported as major prey items of the southern brown bandicoot. Different letters indicate statistically different groups between native, hybrid and blackberry sites as identified by generalised linear mixed models and post-hoc Tukey Honestly Significant Difference (HSD). Bold variables were those used in generalized additive mixed models.

	blackberry		**hybrid**		**native**	
	mean	*SE*	*mean*	*SE*	*mean*	*SE*
vegetation	*n = 15*		*n = 15*		*n = 10*	
veg touches	**245.32^{a}**	**5.15**	**325.33^{b}**	**10.7**	**216.00^{a}**	**10.3**
BB %	**0.49^{a}**	**0.04**	**0.13^{b}**	**0.01**	**0.00^{b}**	**0.00**
DBH (cm)	**13.10^{a}**	**1.80**	**82.67^{b}**	**1.69**	**60.00^{ab}**	**9.60**
EWD touches	**9.45^{ab}**	**0.89**	**6.33^{a}**	**0.65**	**14.50^{b}**	**2.29**
truffle	*n = 12*		*n = 12*		*n = 8*	
truffle diversity	**0.68^{a}**	**0.09**	**0.67^{a}**	**0.08**	**3.15^{b}**	**0.08**
truffle abundance	**1.97^{a}**	**0.39**	**1.33^{a}**	**0.22**	**9.50^{b}**	**0.11**
arthropod	*n = 30*		*n = 30*		*n = 20*	
arthropod diversity	**3.13^{a}**	**0.14**	**2.39^{b}**	**0.10**	**4.08^{c}**	**0.14**
arthropod abundance	**25.88^{a}**	**1.16**	**15.19^{ab}**	**1.67**	**10.79^{b}**	**0.37**

Table 4.3 Total number of truffle samples per genus and site type

Surveys were conducted for four consecutive seasons during 2010–2011 for standardized time periods across one randomly selected 10x20m plot per site (NB. 4 adjoining 10 x 20 m plots were surveyed but these were increasing distances from the drainage line – only the ones in drainage line/blackberry are reported here.) Data were pooled and averaged across these four seasons, and across the four replicate plots per site. Means and standard distribution (SE) are based on data that were further pooled and averaged for each site type.

	blackberry		**hybrid**		**native**	
	n = 12		*n = 12*		*n = 8*	
	mean	*SE*	*mean*	*SE*	*mean*	*SE*
Amarrendia	0.00	0.08	0.00	0.00	0.25	0.25
Chamonixia	0.00	0.00	0.33	0.14	0.50	0.19
Descomyces	0.00	0.00	0.75	0.39	2.00	0.76
Hydnoplicata	0.00	0.00	0.00	0.00	1.50	0.19
Hysterangium	0.67	0.71	0.00	0.00	4.00	0.00
Mesophellia	0.00	0.00	0.00	0.00	0.50	0.19

Table 4.4 Mean captures per season and site type of arthropod orders

The arthropod orders in bold are widely regarded as the major prey items of the southern brown bandicoot (Heinsohn 1966; Quin 1985; Mallick et al. 1998), and were used to calculate arthropod biomass for each site type. Pitfall surveys were conducted at 10 replicate plots per site for four seasons, and data were pooled then averaged across the plots.

	blackberry		**hybrid**		**native**	
	n = 30		*n = 30*		*n = 20*	
	mean	*SE*	*mean*	*SE*	*mean*	*SE*
biomass						
arthropod biomass: 2-5 mm	4.7	0.23	0.21	0.05	0.91	0.20
arthropod biomass: 6-10 mm	86.93	2.91	40.33	4.79	28.27	0.20
arthropod biomass: 11-15 mm	49.67	2.49	58.32	7.09	25.84	1.66
arthropod biomass: >15 mm	61.09	8.57	37.92	3.23	45.59	1.99
orders						
Amphipoda	21.29	11.44	32.88	6.35	0.98	0.98
Araneae	**3.88**	**1.11**	**5.75**	**3.34**	**1.47**	**0.49**
Blattodea	0.00	0.00	0.06	0.06	0.75	0.51
Chilopoda	0.05	0.04	0.12	0.06	0.00	0.00
Coleoptera	**3.14**	**0.52**	**0.55**	**0.38**	**1.82**	**0.41**
Collembola	22.19	7.17	10.30	5.42	0.27	0.27
Dermaptera	0.14	0.14	0.29	0.29	0.80	0.26
Diplopoda	14.46	5.74	4.27	1.91	3.82	3.64
Diptera	0.01	0.01	0.00	0.00	0.00	0.00
Haplotaxida	**1.55**	**0.24**	**1.61**	**0.27**	**1.90**	**0.65**
Hemiptera	1.30	0.90	2.23	0.87	1.47	1.29
Hymenoptera	0.78	0.27	2.05	0.40	3.74	1.19
Isopoda	**1.80**	**1.04**	**0.12**	**0.12**	**0.54**	**0.36**
Lepidoptera	**0.52**	**0.22**	**0.83**	**0.33**	**0.65**	**0.29**
Orthoptera	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**

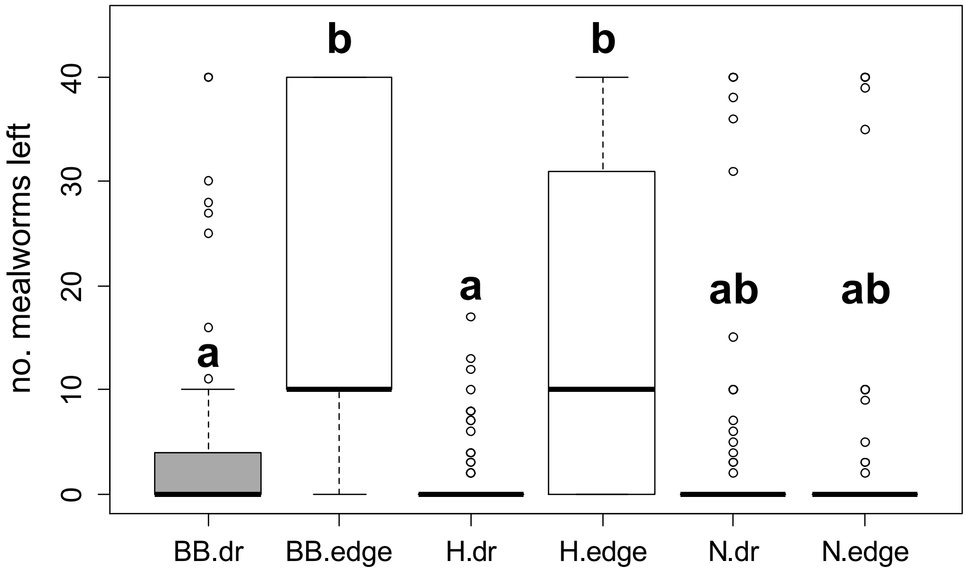


Fig. 4.3 Difference between perceived predation risk based on Giving Up Densities (GUDs)

Number of mealworms left in Giving Up Density (GUD) trays based on 5 nights at 5 sites across native (n = 2), hybrid (n=1) and blackberry-dominated novel (n = 2) sites. Trays were set with 40 mealworms buried under damp sand, and placed in the drainage lines (dr) and 5 m away in the surrounding native vegetation (edge) of blackberry (BB), hybrid (H) and native (N) sites. Different letters indicate statistically significant differences between feed tray locations.

4.3.2 Population fitness and productivity

A total of 241 individual southern brown bandicoots were captured, including 110 females. Breeding occurred across all sites, with 438 pouch young and 111 juveniles observed (22 dependent juveniles < 140 g and 89 independent juveniles ≥ 140 g). Population measures revealed significant differences in demographics and the potential resilience of southern brown bandicoot populations across the site types (Table 4.5). Blackberry sites had 60% more adult females than native sites. The density of adult females was positively influenced by elevated woody debris, blackberry density, arthropod abundance and DBH (>60 cm) in the top-ranked GAMMs (Table 4.6). Of these, only elevated woody debris was a significant indicator when modelled individually (GAMM $P = 0.030$; Table 4.7; Fig. 4.3).

Indicators of individual fitness did not detect any strong trends across the blackberry, hybrid and native sites. Neither the proportion of adult females breeding ($\bar{x} = 0.52$, 0.49 and 0.33 respectively; Table 4.5) nor the number of pouch young per litter ($\bar{x} = 2.26$, 2.39 and 2.26) varied significantly. Although there were no significant differences in the proportion of females breeding, the individual GAMMs identified vegetation density as a marginally significant positive predictor of female reproductive fitness below a threshold of 300 touches per plot (GAMM $P = 0.050$; Tables 4.6 and 4.7; Fig. 4.4). Mean litter size for the southern brown bandicoot has previously been reported as ranging from 2.0 (Lobert 1985) to 3.9 (Stoddart & Braithwaite 1979), with both estimates based on bandicoot populations within the Royal Botanic Gardens Annexe, Cranbourne, in south-eastern Australia. Litter size in the Mount Lofty Ranges has previously been recorded as 3.0 (Paull 1992). The current litter sizes presented here of 2.26–2.39 are therefore at the lower end, but within the normal range, for this species. There were no predictors for the number of pouch young per litter.

Blackberry sites exhibited the highest reproductive output, with 270% more pouch young recorded in blackberry ($\bar{x} = 238$) compared with native sites ($\bar{x} = 86$; Table 4.5). Twenty two pre-dispersal juveniles (51-139 g) were captured without an adult female, and about half of these were recruited into populations at the hybrid and blackberry sites. One pre-dispersal juvenile (66 g) was captured at a native site, but was not re-captured. The density of immature juveniles at blackberry sites ($\bar{x} = 0.96$ ±0.15) was significantly higher than in native sites ($\bar{x} = 0.08$ ±0.05; HSD $P = 0.0123$), but not different to hybrid sites. There was no significant difference in juvenile density between native and hybrid sites (HSD $P = 0.108$). This trend was reflected in the recruitment rates for independent juveniles (> 140 g) that had been weaned at their first capture. The mean number of independent juveniles recruited into the population per season was significantly higher in blackberry ($\bar{x} = 1.99$ ±0.22) compared to native ($\bar{x} = 0.25$ ±0.09; HSD $P < 0.001$) and hybrid ($\bar{x} = 0.96$ ±0.11; HSD $P = 0.0376$) sites. Juveniles were thus 800% more likely to be recruited into the population at blackberry sites

Table 4.5 Differences between bandicoot demographic responses to habitat quality

Differences are given as means and standard distribution (SE) standardised to 100 trap sessions per site per season, based on 8 sites and 11 seasons. Juvenile recruits are the mean number of independent individuals (>140g and <400 g for female and <500g male) captured per site and season that were re-captured in at least one subsequent season, and so were considered recruits into the population. Captures from the first and last season were excluded as it was not possible to determine whether each individual was a recruit or non-recruit. Responses in bold were used in modelling. Bold values with different letters indicate statistical differences calculated by Tukey Honestly Significant Difference (HSD).

	blackberry		**hybrid**		**native**	
	n = 7982		*n = 8080*		*n = 5288*	
	mean	*SE*	*mean*	*SE*	*mean*	*SE*
individual						
pouch young/litter	2.26^{a}	0.14	2.39^{a}	0.14	2.26^{a}	0.15
population						
adult female density per site	2.06^{a}	0.2	0.91^{a}	0.13	1.23^{a}	0.28
proportion of adult females breeding per site	0.52^{a}	0.07	0.49^{a}	0.08	0.33^{a}	0.09
pouch young per site	0.75^{a}	0.09	0.79^{a}	0.11	0.41^{a}	0.08
immature juveniles (<140 g) per site	**0.96^{a}**	**0.15**	**0.49^{ab}**	**0.12**	**0.08^{b}**	**0.05**
independent juveniles (>140 g) recruited per site	**1.99^{a}**	**0.22**	**0.96^{b}**	**0.11**	**0.25^{c}**	**0.09**

Table 4.6 Top-ranked models (Δ <2.00) for generalized additive mixed models (GAMMs) of bandicoot reproductive responses to key habitat characteristics.

GAMMs based on 11 seasons across 8 sites. Full candidate GAMMs were generated with Laplace approximation for vegetation density, blackberry as % of vegetation density, DBH, elevated woody debris and arthropod abundance as explanatory variables. Site was specified as random factor for adult female density, and site nested within year and year*season for all other responses. GAMMs were generated with Gaussian distribution and identity link function for the proportion of females breeding, and with Poisson distribution and log link function for the other three response variables. Only the strongest models with Δ < 2.00 are presented.

site					
rank	*model*	*AICc*	Δ	*weight*	*R ^{2}(adj)*
individual					
pouch young per litter					
1	NULL	-5.04	14.31	0.00	0.00
population					
female density					
1	BB + EWD	65.64	0.00	0.33	0.58
2	arthro + BB + EWD	67.15	1.52	0.15	0.59
3	BB + DBH	67.23	1.60	0.15	0.57
proportion of females breeding					
1	NULL	82.33	0.00	0.37	0.00
2	VEG	83.38	1.04	0.22	
recruits					
1	BB + EWD	67.94	0.00	0.39	0.54

Table 4.7 GAMM estimates calculated for each explanatory individually

GAMMs estimates based on 11 seasons across 8 sites for the interaction between each explanatory variable and bandicoot response individually. Full candidate GAMMs were generated with Laplace approximation for arthropod abundance, vegetation density, blackberry as % of vegetation density, DBH and elevated woody debris as explanatory variables. Site was specified as random factor for adult female density, and site nested within year and year*season for all other responses. GAMMs were generated with Gaussian distribution and identity link function for the proportion of females breeding, and with Poisson distribution and log link function for the other three response variables.

	proportion of females breeding			**pouch young per litter**			**female density**			**juvenile recruitment**		
	test statistic	*R^2 (adj)*	*P*	*test statistic*	*R^2 (adj)*	*P*	*test statistic*	*R^2 (adj)*	*P*	*test statistic*	*R^2 (adj)*	*P*
arthropod abundance	1.901	0.0097	0.234	0.41	0.02	0.524	2.05	0.16	0.152	**12.07**	**0.44**	**<0.001**
VEG	**5.61**	**0.05**	**0.050**	0.12	0.00	0.735	1.52	0.07	0.368	0.16	0.00	0.689
BB	0.87	0.00	0.385	0.38	0.02	0.540	1.54	0.07	0.227	**14.75**	**0.37**	**<0.001**
DBH	0.35	0.00	0.556	0.16	0.00	0.688	5.34	0.33	0.062	3.65	0.20	0.056
EWD	0.38	0.00	0.536	0.01	0.00	0.939	**4.94**	**0.20**	**0.030**	**11.95**	**0.27**	**0.002**

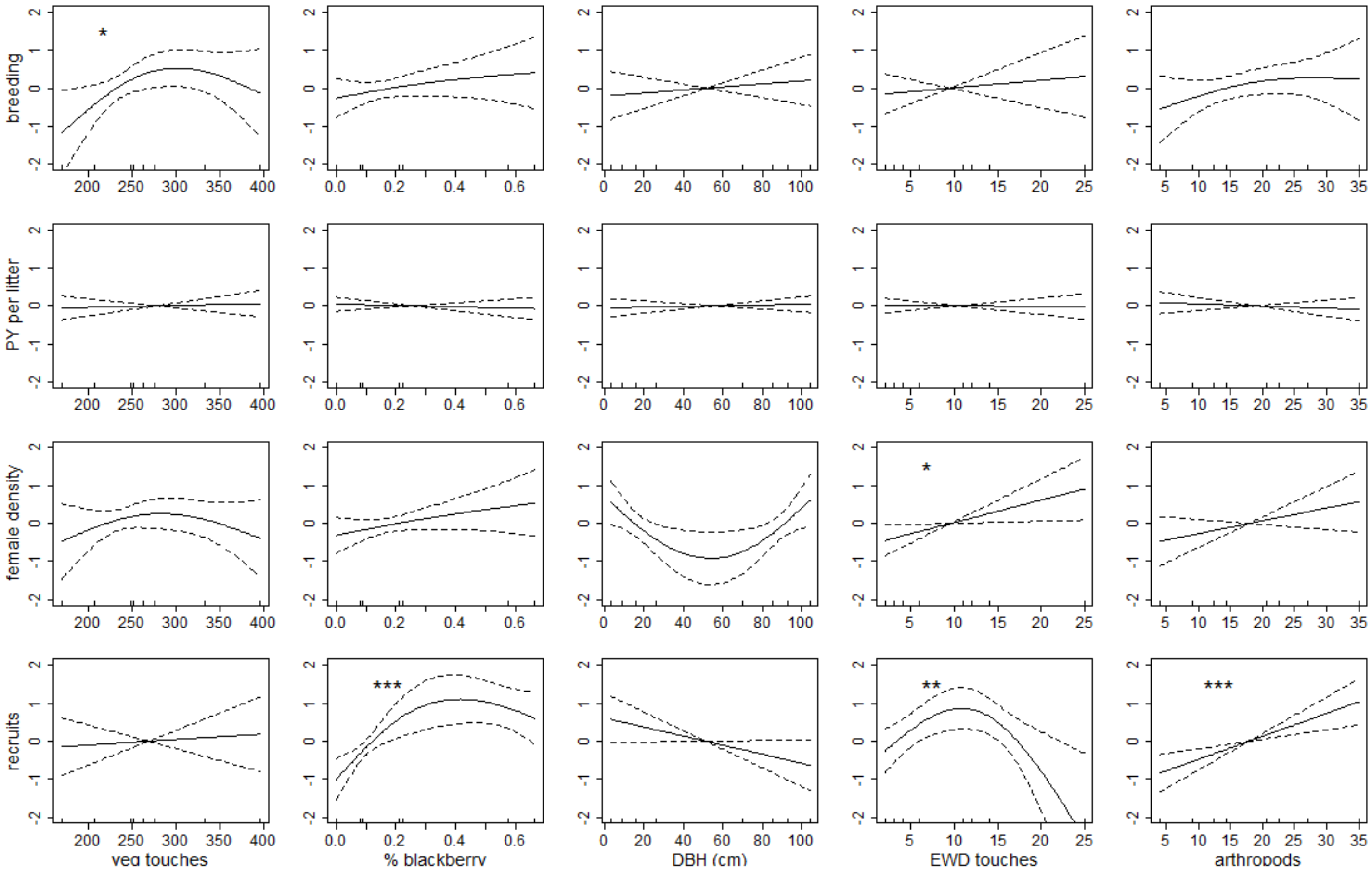


Fig. 4.4 GAMM plots of bandicoot demographic responses to indicators of habitat quality

The plots give the estimated smoothing curves for GAM models of bandicoot demographics across 8 sites and 11 seasons. y axis is the effect of explanatory variables on bandicoot response. x-axis represents the no. of individuals; dashed lines are the ±2 SE confidence bands. p values and R^2 scores are given for significant relationships. R2 scores are from top-ranked models (Δ <2.00) where that variable was specified individually. * *p* ≤0.05, ***p*≤0.01, ****p*≤0.001 are from GAMM estimates calculated for each explanatory variable individually.

compared to native sites (HSD *P* <0.001). Only one GAMM was a strong model, indicating that recruitment of independent juveniles into the population was influenced by the proportion of blackberry (<40%; GAMMR^2 = 0.37, *P* < 0.001) and density of elevated woody debris (≤ 10 touches per plot; GAMM R^2 = 0.27,*P* = 0.002; Table 4.6 and 4.7; Fig. 4.4). The individual GAMMs also identified arthropod abundance as a positive predictor for recruitment (GAMM R^2 = 0.44, *P* = <0.001). Overall, population measures performed much better as demographic predictors than individual measures, and therefore gave greater insight into population trends across the native, hybrid and novel blackberry-dominated ecosystems of the Mount Lofty Ranges.

4.4 Discussion

Understanding the net effect of biological invasions is an essential pre-requisite for successfully restoring the native ecosystems they alter. Our research shows that contrary to the dominant view of non-native plants being a threat to native biodiversity, they can sometimes play a critical role in facilitating dispersal and recruitment within fauna meta-populations. This interaction is particularly important where there is limited recruitment within the native patches remaining within fragmented landscapes. The reproductive success of the southern brown bandicoot was significantly higher in blackberry-dominated systems compared to native ecosystems. Blackberry improved habitat quality and population persistence for the southern brown bandicoot in novel ecosystems by: (1) modifying habitat as an ecological engineer; (2) providing increased abundance of arthropods as a food resource; and (3) increasing the availability of shelter and protection from predators where there is otherwise little cover.

4.4.1 Facilitator of habitat quality

Previous research (Chapter 2) identified blackberry as an ecosystem engineer that creates habitat for small mammals, including the southern brown bandicoot, by increasing vegetation structure and density in novel ecosystems where they might not persist otherwise. The current study builds on this research and has shown that recruitment of juvenile southern brown bandicoots is significantly higher in blackberry systems and is strongly predicted by both blackberry density and arthropod abundance.

Southern brown bandicoots are regarded as opportunistic generalists and adjust their diet depending on the food resources available (Broughton & Dickman 1991; Reese 2000). Broughton and Dickman (1991) found that individual southern brown bandicoots expanded their home range to take advantage of supplementary food, suggesting that bandicoots can detect rich food resources outside their home range and disperse or expand their territory to access them. Further, southern brown bandicoots will eat millipedes, scorpions, centipedes and bull ants when rainfall is low and there is limited availability of their preferred arthropod prey (Lobert & Lee 1990; see also Broughton & Dickman 1991). The availability and abundance of arthropods is strongly correlated with bandicoot breeding activity (Lobert & Lee 1990), and is known to interact with vegetation density to influence southern brown bandicoot abundance (Lobert 1985). Although the diversity of arthropods was lower in novel ecosystems, the overall abundance was higher and clearly provides adequate resources to trigger and support breeding. Individual fitness of southern brown bandicoots was comparable across all site types (% females breeding and pouch young per litter in this chapter, and haematology in Chapter 3), indicating that bandicoots are accessing enough resources to support breeding. The comparable individual fitness suggests that the nutritional status and health condition of bandicoots may be similar across blackberry and native ecosystems and warrants further investigation.

4.4.2 Ranking the influence of habitat thresholds on population persistence

Productivity of southern brown bandicoots, based on juvenile recruitment, was by far the highest in the blackberry. The net effect of reproductive success was positive in blackberry habitat but negative in native vegetation. This suggests that although individual females breed when vegetation density is adequate, dense vegetation with abundant food resources facilitates higher juvenile survival and, in turn, recruitment into the population. Several studies have found that younger age classes tend to consume small prey (Whitfield & Donnelly 2006; Meynier et al. 2008; Maragno & Souza 2011). The abundant supply of small arthropods may therefore provide a readily available food resource for juvenile bandicoots, while the blackberry habitat provides protection from predators when bandicoots are most vulnerable during the dispersal of juveniles (Lobert & Lee 1990). Similarly, Snelling (2007) reported that the greatest density of southern brown bandicoot diggings was <20 m from blackberry thickets when the surrounding vegetation was sparse in the Mount Lofty Ranges. Further, GUD trials in the present study found that bandicoots foraged more often and consumed more mealworms within the protection of blackberry compared with 5 m away in sparse native vegetation. This suggests that blackberry increased the shelter and protection for bandicoots in novel ecosystems.

Overall, the GUD trials confirmed that bandicoot perceptions of predation risk reflected the protective cover of vegetation, as vegetation density was highest (Chapter 2) and predation risk appears to be lowest along hybrid drainage lines. Vegetation density was therefore used as a proxy for the level of predation risk perceived by southern brown bandicoots in this system. A number of ecological thresholds were identified in the influence of habitat variables on juvenile recruitment. Vegetation density itself had no influence in the top-ranked GAM models, nor did it have any predictive power in the individual GAMMs (R^2 = 0.00, P = 0.689). Blackberry was identified as the strongest predictor of recruitment overall: the combination of blackberry and elevated woody debris was the only strong model identified by the model ranking process, and blackberry (40% of total vegetation density) accounted for 37% of model deviance (P <0.001) by itself. Arthropod abundance was the second highest predictor of juvenile recruitment, and hence southern brown bandicoot persistence in the region. Arthropods explained 44% of deviance (P <0.001), while elevated woody debris (≤10 touches per plot) was the third strongest predictor (top-ranked model with blackberry R^2 = 54%; individual GAMM R^2 = 27%, P = 0.002). Other GUD studies have reported that small mammals such as fox squirrels (*Sciurus carolinensis*; Brown 1999), common voles (*Microtus arvalis*; Jacob & Brown 2000) and yellow-footed antechinus (*Antechinus flavipes;* Stokes et al. 2004) demonstrate significantly lower predation risk when native vegetation or artificial cover is available. Similarly, Pickett et al. (2005) found that brushtail possums (*Trichosurus vulpecula*) travelled further on the ground and had lower GUD thresholds at sites where red fox (*Vulpes vulpes*) had been removed. By increasing access to abundant food resources and protection from predators for independent juveniles while they are dispersing and at their most vulnerable, blackberry improves the habitat quality and connectivity for southern brown bandicoots. Blackberry-dominated novel ecosystems are therefore supporting source populations of the endangered southern brown bandicoot that may be critical for the persistence of the meta-population across the highly fragmented landscape of the Mount Lofty Ranges.

4.4.3 Future research directions

Native sites in the Mount Lofty Ranges appear to be currently operating as population sinks for southern brown bandicoots, with recruitment ranging from minimal to nil across the different native sites. This is the first time sink populations of native fauna have been documented in remnant native ecosystems compared with source populations from the surrounding matrix of novel ecosystems which are dominated by non-native blackberry. Southern brown bandicoots persisting in these native sites are therefore most likely to be vulnerable to stochastic events and to contribute less to the genetic diversity and resilience of the meta-population. Blackberry, on the other hand, apparently acts as the population source in novel ecosystems, and therefore needs to be managed appropriately across the 'canary landscape' of the Mount Lofty Ranges.

Our research confirms that invasive species can act as ecological engineers to create habitat that not only retains the diversity and abundance of native fauna in novel ecosystems where they would otherwise become locally extinct, but is also critical for recruitment and population persistence. Further research is now needed to identify the effect of blackberry on the population viability and persistence of southern brown bandicoot meta-populations at a landscape scale. Finally, environmental conditions are known to have a strong influence on the breeding activity of bandicoots, particularly temperature and day length (Barnes & Gemmell 1984; Paull 2003; Paull et al. 2013), but their interaction with the beneficial effects of blackberry on habitat quality and population persistence is unknown.

Chapter 5 Framework for quantifying the response of native fauna to non-native plants

5.1 Overview

Non-native species impact on natural ecosystems worldwide. In many systems this impact is overwhelmingly negative and poses a significant threat to native biodiversity, while in others the interactions are more complex and may also be beneficial (Sax et al. 2007; Davis et al. 2011; Schlaepfer et al. 2011). Previous reviews and frameworks on different aspects of these native – non-native interactions are critiqued in this final chapter to clarify the research gaps addressed by the present research. One of the major gaps is the need for a conservation and restoration assessment framework that addresses beneficial as well as threatening processes associated with non-native plants. The second section of this chapter presents a conceptual framework of principles in response to this gap, and as a foundation for the impact assessment framework that follows. Chapters 2–4 tested a range of approaches to quantify the response of small native mammals to non-native blackberry. Specifically, the thesis has examined the effect of blackberry on habitat resources that are important for small mammals at microhabitat and site scales. By using the same habitat characteristics as explanatory variables throughout this study, differences in the response of small mammals have been quantified at community (Chapter 2), population (Chapter 4) and individual levels (Chapters 3 and 4). Importantly, this consistent modelling approach has enabled a comparative analysis of the different response variables to be presented in this final chapter as part of an impact assessment framework. The framework outlines what to include in quantitative assessments of native fauna and non-native plant interactions to guide evidence-based conservation and restoration planning. The final sections in this concluding chapter propose future research priorities and highlight the implications for conservation management where non-native plants provide critical habitat for native fauna.

5.2 Existing frameworks on native – non-native interactions

Reviews by Hobbs et al. (2009), Schlaepfer et al. (2011), and Rodriguez (2006) provided an overarching conceptual view for the research presented in this research, while the numerous published case studies of native–non-native biodiversity interactions highlighted the diversity and complexity of these interactions. It was not possible to identify any models to guide and quantify the assessment of non-native plant impacts on native fauna. The need for improved quantitative assessments of native responses to non-native species has also been identified by Kueffer and Daehler (2009) and Hulme et al. (2013). A critique of existing frameworks is therefore presented here in an effort to integrate them and highlight the gaps where further research is required. The approaches adopted by the existing conceptual frameworks fall into three categories: landscape-scale focus; non-native focus; and native focus.

5.2.1 Focus on landscape scale

Publications by Hobbs et al. (2006; 2009) and Kueffer and Daehler (2009) provide complementary frameworks that offer a landscape-scale approach for non-native species interactions within human-altered ecosystems. The model presented by Hobbs et al. (2009) focuses on three ecosystem types that may result from biotic (including biological invasion) and/or abiotic change triggering transition through different ecological states. This model provided the main conceptual approach for the present research, with three site types representing the historic ('native'), hybrid and novel ('blackberry') transition states. The importance of understanding and managing novel ecosystems for conservation has been growing steadily (Lindenmayer et al. 2008a; Seastedt et al. 2008; Bridgewater et al. 2011; Davis et al. 2011), yet many gaps remain in transforming the Hobbs et al. (2009) framework into quantitative assessments and effective management of non-native impacts in novel ecosystems (Hobbs et al. 2013).

Likewise, the Habitat Classification Framework developed by Kueffer and Duehler (2009) corresponds with the broader Hobbs et al. (2009) model and defines ecosystem types specifically associated with biological invasion. While both frameworks identify habitat as core or disturbed matrix, the Kueffer and Daehler (2009) model focuses on the biotic change identified by Hobbs et al. (2006). Three of the ecosystem types match Hobbs et al. (2009), and the fourth designates habitat that is defined by a high level of human intervention that overlaps the hybrid and novel ecosystems. This additional spectrum of human influence, and the resulting matrix, means the framework provides a useful context for non-native species research. More recently, Kueffer and Kaiser-Bunbury (2013) have built on the Kueffer and Daehler (2009) model and propose a conceptual framework for biodiversity conservation that is based on three dimensions of human influence: (1) degree of anthropogenic change, from historic to novel; (2) degree of human influence, from deliberate to inadvertent (e.g. climate change); and (3) land-use priority, from biodiversity conservation to production. While both models developed by Kueffer (Kueffer & Daehler 2009; Kueffer & Kaiser-Bunbury 2013) have been useful in developing and reflecting on the present research, Hobbs et al. (2009) was used as the overarching framework because their transition states characterised the spectrum from native to novel ecosystems observed in the study site, the Mount Lofty Ranges.

The next level of consideration was to identify the ecological roles of non-native species at the landscape scale. Schlaepfer et al. (2011) identified six roles of non-native species that may have degrading and/or beneficial effects on native biodiversity: habitat modification (particularly food and shelter); restoration catalyst; ecosystem engineering; ecosystem service facilitation; taxon substitution; and species preservation. Overall, the intentionally landscape-scale frameworks described by Hobbs et al. (2009), Kueffer and Daehler (2009) and Schlaepfer et al. (2011) provide important insight that can be complemented by more detailed models to quantify the net effect of interactions between native and non-native species.

5.2.2 Focus on non-native species

Rodriguez (2006) provided a framework that addresses some of the gaps of the landscape-scale approach by examining the how, when and why of non-native impacts on native biodiversity. This approach focuses primarily on non-native species. As the most comprehensive of non-native species frameworks identified, it provides both a conceptual scaffold and detailed model for assessing the nature of non-native interactions. The strength of this framework is the depth and breadth of its scope, yet some of the complexity and language may challenge some readers. For example, Shackelford et al. (2013) highlighted the importance of presenting frameworks that are accessible and useful for a broad range of audiences, from community groups to policy advisors. A further limitation may be the intentionally singular focus on the positive facilitative effects of non-native species, when the overwhelming majority of studies in this field continue to identify negative impacts (Vitule et al. 2012). Despite these challenges, the Rodriguez (2006) model was the most useful in understanding the beneficial dynamics identified in the study system.

5.2.3 Focus on native species

The final approach is focused on the response of native species. Martin & Murray (2011) provide the only conceptual framework identified at this level, and they focus on the response of reptiles and amphibians to non-native plants. Their predictive framework integrates three mechanistic models to predict how non-native plants will impact on reptile and amphibian assemblages: habitat modification; herbivory and predator–prey interactions; and reproductive success. The native focus strengthens this framework as it draws attention to focal communities and species, and opportunities for maximising conservation and habitat restoration, rather than focusing primarily on controlling invasive species. A further advantage is the use of empirical evidence to develop mechanistic predictions that have previously been tested, and can be further investigated. However, one of the restrictions of this framework is the limited distinction between explanatory variables (plant-related) and response variables (fauna-related) for the mechanistic predictions. Of the three mechanistic models, one focuses entirely on the explanatory variables of habitat modification, the second combines explanatory (availability of plant resources for herbivory) with response (herbivore behaviour and predator–prey behaviour), and the third focuses on reproductive responses by females. This blurring of explanatory and response variables limits the scope for comparing predictions across the three mechanistic models. For example, it is not possible in the present case to directly compare the degree of effect of habitat modification (e.g. vegetation density, a potential explanatory variable for population persistence) with the direct effect of reduced reproductive success in bandicoots(e.g. young recruited per unit area, a response variable and population indicator) in predicting the extinction risk for fauna populations. Despite this limitation, the mechanistic and testable aspects of the framework provide a solid base and could be revised and extended as a broader framework to assess the impact of non-native flora on all native fauna.

Understandably, no single framework on non-native – native interactions can cover all aspects from the broad conceptual to detailed assessment methods. Each has its own insights and limitations. Overall, there is a lack of overarching conceptual frameworks to guide quantitative assessments of native fauna responses to non-native species. Without a guiding framework, assessments are less likely to address the critical conservation questions through targeted and robust survey design, and consequently have limited value as a management tool. Reid et al. (2009) identified a similar lack of, and need for, impact assessments of the response of native plants to non-native plant management. They reported that 51% of land manager respondents monitored the response of native plants to their restoration activities, and only 33% observed these communities recovering after removal of the target non-native plant. More recently, Shackelford et al. (2013) and Wortley et al. (2013) reported the need for a consistent and clear framework to guide assessment of the response of native biodiversity to restoration activities. These studies highlight the importance of understanding the systems that are the target of conservation and restoration management, and the challenges faced in developing frameworks to assess the complex interactions involved. The present research seeks to address this gap by presenting a framework that brings together a range of approaches across multiple scales and hierarchies to quantify the net response of native fauna to non-native plants. Fauna responses to non-native plants have been modelled, evaluated and predicted across 15 different parameters. These measures ranged from broad-scale community richness to the reproductive fitness of individuals (Table 5.1). These parameters form the basis of an evidence-based framework that can then be used to guide conservation and restoration decision-making where native fauna are using non-native plants as habitat.

Table 5. 1 Description of response variables modelled at each hierarchical level in the present study.

hierarchical level	**response variable**
community assemblage	species richness Simpson diversity bush rat abundance brushtail possum abundance southern brown bandicoot abundance yellow-footed antechinus abundance
haematology of southern brown bandicoot	neutrophils lymphocytes neutrophil / lymphocyte ratio eosinophils polychromatophils
demographics of southern brown bandicoot	female density % females breeding pouch young per litter juvenile recruitment

This present investigation has extended beyond the primary data to: (1) evaluate which approaches may be broadly useful for assessing native fauna and non-native plant interactions; and (2) develop a model that encapsulates both the explanatory variables of non-native plant impact on habitat and the fauna response variables to assess the net effect of these interactions. Three overarching principles for ecosystem restoration are presented in the next section as a basis for considering which assessment and review methods may be most useful for different ecological contexts. A model is then presented to guide future quantitative assessments of the net effect of fauna responses to native plant interactions, including a comparative analysis of methods used in the present study and elsewhere to quantify the effect of non-native plants on native fauna.

5.3 Overarching principles for restoring ecosystem resilience

Ecological restoration is widely recognised as an integral component of conservation both locally and globally (Society for Ecological Restoration 2004; Shackelford et al. 2013) and it plays an important role in mitigating the negative effects of non-native plants on native biodiversity. While the need and broad principles for ecological restoration are well documented, there is much less consensus on: when restoration is necessary and likely to be effective, how to optimise restoration strategies to achieve the best ecological outcomes, and how to measure restoration success and improve strategies within an adaptive management approach (Suding 2011; Shackelford et al. 2013; Wortley et al. 2013). Growing evidence suggests that current approaches to managing non-native plants may, in some circumstances, be poorly targeted and/or sometimes entirely unwarranted (Downey 2010; Downey et al. 2010; Hulme et al. 2013). Hulme et al. (2013) suggest this gap is largely due to the absence of a consistent and overarching hypothesis to guide research internationally on non-native impacts. They therefore argue for the development of an overarching restoration framework and improved quantitative evidence to guide non-native plant management. The research presented in Chapters 2–4 highlights the importance of a holistic approach that restores resilience to ecosystems by responding to the net effects of non-native plants. A conceptual framework outlining the aims and principles for restoration is therefore presented here (Fig. 5.1), and provides the foundation for the framework on impact assessments that follows in the next section.

Restoration activities are diverse and may be focused on achieving one or more goals. These goals have traditionally included restoring ecosystems to some historic state, removing non-native plants, and managing any other disturbance processes (eg. erosion, fire). The importance of restoring resilience, or stability, to ecosystems is being increasingly recognised as a central theme for ecological restoration (Seastedt et al. 2008; Thorpe & Stanley 2011; Shackelford et al. 2013; Wortley et al. 2013). Thorpe and Stanley (2011) argued that restoration should balance the re-building of historic systems with building resilient systems for the future. Resilient landscapes are those with communities and ecosystems that are viable over time despite variable environmental conditions (e.g. climate and fire; Seastedt et al. 2008). Three principles are proposed here to guide restoration activities towards this central aim of ecosystem resilience: retain, reduce, and review.

5.3.1 Retain

The primary principles for restoration planning should be the retention of diversity and complexity in the ecological patterns and processes across multiple scales (Leopold 1949; Fischer et al. 2006; Thorpe & Stanley 2011; Shackelford et al. 2013). Pattern-oriented approaches to restoration are multi-scale and aim to retain: landscape heterogeneity (e.g.heterogeneous environmental gradients and diverse vegetation communities; Fischer et al. 2006; Shackelford et al. 2013), genetic diversity (Fischer et al. 2006; Seastedt et al. 2008; e.g. through refugia, buffers and vegetation linkages at landscape scale; Cadotte 2011; Cadotte et al. 2011; Plieninger & Gaertner 2011; Catford 2013), and structural complexity of vegetation and fauna habitat at site and microhabitat scales (e.g. extensive patches of structurally complex native vegetation, rocks and logs remain in-situ; Fischer et al. 2006; Barton et al. 2011; Catford 2013). Process-oriented approaches, on the other hand, are concerned with restoring the ecological processes of a system (Fischer et al. 2006; Shackelford et al. 2013). Processes within resilient ecosystems and landscapes include: biogeochemical configurations (Catford 2013), ecosystem functioning (Shackelford et al. 2013), interactions arising from functional and species diversity in microbial through to vertebrate communities (Fischer et al. 2006; Seastedt et al. 2008; Cadotte 2011; Cadotte et al. 2011; Plieninger & Gaertner 2011; Catford 2013; Novoa et al. 2013), and appropriate disturbance regimes and succession stages (Fischer et al. 2006). Retention-focused approaches may also harness opportunities for natives by identifying areas within, or along the edges of, non-native plant that can be managed to increase the regeneration and competitiveness of native plants (Wilson 1994; Kueffer et al. 2010)

5.3.2 Reduce

Once the primary principle of retaining beneficial ecosystem patterns and processes has been applied to develop appropriate restoration strategies, the secondary principle of reducing negative interactions can be addressed (Leopold 1949; Fischer et al. 2006). Negative effects to be reduced include threatening ecosystem-specific processes and aggressive, over-abundant and/or invasive species (Fischer et al. 2006; Plieninger & Gaertner 2011). Restoration strategies that seek to restore resilience by reducing negative interactions need to be undertaken gradually to avoid inadvertently triggering further negative effects.

5.3.3 Review

The third principle for ecosystem restoration is review. This principle promotes sophisticated "first, do no harm" and evidence-based approaches (Sogge et al. 2008) that are based on gradual adaptive management, monitoring and ongoing review (Seastedt et al. 2008; Reid et al. 2009). It is important that restoration goals are tailored to the complex interactions of the particular ecosystems (Shackelford et al. 2013) as well as the capacity of those involved in the restoration (Ewing et al. 2013).

These three principles of retain, reduce and review provide a foundation for restoration approaches. The next step is to assess the net effect of non-native plants to identify what needs to be retained and reduced through restoration for the unique context of each ecosystem.

Figure 5.1 Framework of principles to guide restoration of native vegetation where non-native plants are present

The framework provides principles to guide management actions in restoring resilience to disturbed ecosystems and landscapes, particularly where non-native plants are providing critical ecosystem processes. Resilience is the central aim, with the 3 R's of retain, reduce and review based on an ongoing adaptive management approach.

5.4 Framework to assess the net effect of native fauna responses to non-native plants

Studies on the effect of non-native plants on native fauna have traditionally adopted a community level approach. The majority of previous studies have assessed non-native plant impacts based on native faunal composition, richness, diversity and/or abundance (Crooks 2002; Castilla et al. 2004; Schlaepfer et al. 2011). Drawing on the foundations of existing frameworks and insights gained from the present research, this section presents a framework to offer further progress towards quantitative and multi-scale assessments of native fauna responses to non-native plants in novel ecosystems (Hulme et al. 2013). The framework seeks to differentiate between the two major drivers of fauna responses (habitat and fauna interactions), and the four hierarchical levels (individual, population, community and functional group) at which fauna respond to non-native plants across the disturbance spectrum (Fig. 5.2). This thesis examined the effect of non-native plants on the persistence of native fauna in human-altered systems from multiple perspectives, and assessed the contribution of each approach by using the same explanatory habitat variables throughout. The framework deals with novel ecosystems because non-native plants are considered to be a significant component of these systems, and are therefore likely to have variable yet significant effects on fauna persisting within them (Hobbs et al. 2009). Remnant ecosystems, on the other hand, may have non-native species present at very low levels, but these are unlikely to impact on native fauna significantly.

The major drivers, or explanatory variables, in this framework are those that result directly from the presence of non-native plants. The first group are the primary physical resources provided in habitat created by non-native plants, particularly food and shelter. These resources may be altered or novel, and may complement or replace food and shelter resources provided in remnant ecosystems (Chapter 2; Rodriguez 2006; Schlaepfer et al. 2011). The second group are the secondary level of fauna interactions that result from shifts in the primary resources available in non-native habitat. This group includes competition and predation but not herbivory as this is a fauna response at the individual level (with non-native plants as a food resource). Non-native plants can alter interspecific competition within fauna communities as well as predation risk for prey species (Chapter 2).

The second part of the framework outlines the four levels at which native fauna may respond to non-native plants: individual, population, community and functional levels. Responses at the individual level include: patterns of movement (e.g. daily foraging patterns or seasonal dispersal); diet; and fitness (e.g. haematological, biochemistry and reproductive parameters such as young produced and recruited per female).

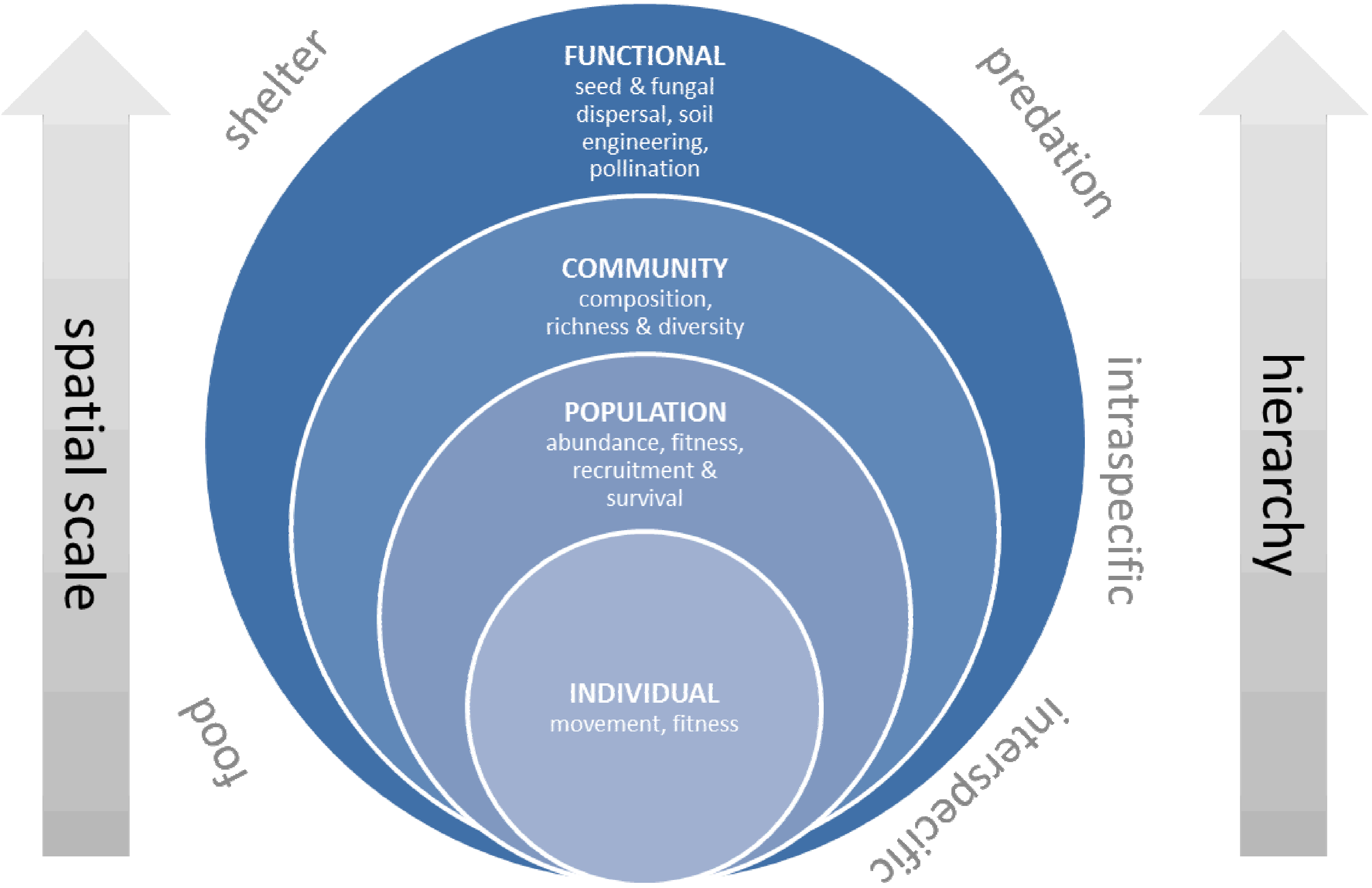


Figure 5.2 Framework to quantify the response of native fauna to non-native plants across multiple scales and hierarchies

Explanatory factors that influence fauna responses to non-native plants are shown outside the circles, the fauna responses at different hierarchical levels are detailed within the nested circles. Assessing fauna responses across multiple hierarchies and scales will increase the reliability of the assessment. .

The physiological parameters are particularly important in assessing habitat quality as they can act as early warning signals and identify trends before these are able to be detected at a population level through reproductive measures. Chapter 3 adopted a conservation physiology approach to assess the impact of non-native plants, and found blackberry was associated with increased chronic stress levels for the southern brown bandicoot. Further, several of the haematological parameters were considerably different to the published reference ranges from the only other study of southern brown bandicoot haematology (Wicks & Clark 2005a). The findings indicate the meta-population of bandicoots persisting within woodlands of the Mount Lofty Ranges may be experiencing higher levels of injury and low grade disease than in the predator-free woodland studied by Wicks and Clark (2005a). This is consistent with previous claims that haematological, and other physiological indicators, may act as early warning signals or 'biomarkers' of ecological change and environmental stressors (Davis et al. 2008; Cooke & O'Connor 2010; Ellis et al. 2012). For example, by using physiological tools to investigate a drastic decline in red-legged kittiwake, a seabird population in the North Pacific, Kitaysky et al. (2006) identified nutritional stress from lipid-poor food resources as the predictor for low recruitment levels. Similarly, reduced reproductive performance of tits in remnant patches adjacent to urban areas has been linked to higher stress hormone levels in breeding females and consequently reduced juvenile condition (Isaksson et al. 2005; Hedblom & Soderstrom 2012). The detailed resolution and predictive power offered by physiological indicators are proving to be particularly useful for human-altered landscapes where environmental change can lead to rapid and devastating impacts that trigger significant disease, mortality and fecundity concerns and put wildlife populations at significant risk (Brearley et al. 2013). For this reason, conservation physiology approaches have significant potential for detecting impacts on fauna populations before they can be identified in reproductive indicators. Physiological biomarkers may therefore be more sensitive and reliable indicators than productivity and recruitment in some contexts, and are highly recommend for quantitative assessments of non-native plant impacts on native fauna.

At the population scale, traditional indicators include abundance and density measures of fauna populations. Population parameters also incorporate more recently emerging measures such as fitness (e.g. young produced per population), productivity (e.g. survivorship and juvenile recruitment at critical life stages per population and area), and genetic composition (e.g. degree of structure within and between populations). For example, reproductive success (e.g. young sub-adults per female) has been used successfully as a proxy for individual female fitness (Mosser et al. 2009). Chapter 4 combined a range of individual and population-level response variables of bandicoots. Overall, population productivity (juvenile recruitment) overwhelmingly provided the most indicative measure of habitat quality and population persistence for the southern brown bandicoot across the spectrum from novel to native ecosystems. In addition, using a combination of population measures gives greater insight into whether populations are acting as source, sink or ecological trap and the direction of the population trends. Blackberry sites produced 270% more pouch young than native sites across the three years of this study. Differential survival and recruitment levels of juveniles at native and blackberry sites further translated to an eight-fold higher recruitment of pouch young at blackberry sites.

These findings are consistent with the work of Mosser et al. (2009) who found that individual female reproductive success (cubs recruited as yearlings per female) was the most reliable indicator of habitat quality for lions in the Serengeti, followed by population productivity (yearling cubs per km^2). Juvenile recruitment per female incorporated both the fitness of individual adult females and the survival of juveniles, and identified river junctions as the highest quality habitat. Although female density and population productivity were associated with rivers, they were also correlated more generally with dense shelter sites and rainfall during the dry season. However, dense shelter sites proved to be misleading indicators of high quality habitat as they were refuges within otherwise open areas inhabited by sink populations. Recruitment is therefore an important indicator of population persistence. Unfortunately, however, the life history traits of the study species in the present research limit the opportunity to test individual female productivity (pouch young per female recruited into population as sub-adults) as an indicator of habitat quality and population persistence. In particular, the small body size, cryptic nature, predator avoidance and high dispersal rates of bush rats, yellow-footed antechinus and southern brown bandicoots would make it virtually impossible to track individual pouch young from a specific female to recruitment as sub-adults into the population. Mosser et al. (2009) concluded that density may be a misleading indicator that fails to distinguish between high quality source habitat and low quality sinks. They found that lions were using the best quality habitat within low-quality sinks, but these areas merely provided refuges for effectively non-reproductive females. My results further support the view that density may be a misleading indicator as no significant differences were detected in female density between site types across the study system. Instead, reproductive success based on juvenile recruitment per unit area proved to be the most useful indicator of demographic trends and population persistence for the southern brown bandicoot.

Community-level measures include species composition, richness and diversity and are currently the most widely used indicators of non-native species impact on native fauna. Chapter 2 investigated the response of small native mammals to blackberry at a community level. Species diversity provided a more sensitive and indicative measure than species richness. Habitat characteristics had no significant influence on species richness, but vegetation density increased diversity at the microhabitat scale and blackberry increased it at site scale. In contrast, Pethiyagoda and Manamendra-Arachchi (2012) found species richness of frogs was lower in novel areas than forest, but still most species had adapted to using the novel ecosystem. Abundance provided clear evidence for species with large sample sizes in the present study, but was limited for rarer species such as the brushtail possum. The combination of microhabitat and site scale investigations complemented each other, and collectively provided important insight into fauna responses. Bandicoot abundance also provided a useful reference point for other more detailed measures of bandicoot responses in Chapters 3 and 4. The combination of community assemblage and focal species provided insight into the broader impact of blackberry on native ecosystems. Overall then, species diversity provides an important overview of the impact of non-native plants across multiple species.

Finally, functional groups are emerging as a useful broader scale at which to assess ecological processes impacted upon by non-native plants (Hulme et al. 2013). In particular, functional groups have the potential to collectively influence novel ecosystems through ecological processes such as: pollination (Goldingay et al. 1987; Williams et al. 2011); soil engineering (Garkaklis et al. 2003, 2004; Valentine et al. 2013); seed dispersal (Schiffman 1994); promotion of mycorrhizal associations through fungal dispersal (Claridge & May 1994; Claridge 2002); and floristic regeneration (Murphy et al. 2005; Neilan et al. 2006), although none of these functional roles where specifically addressed here.

Most importantly, no single measure or scale can explain or predict the complex responses of native fauna to non-native plants. Different response measures are useful for investigating different questions about habitat quality, including different aspects of non-native plant impacts on native fauna (Pidgeon et al. 2006). The mixed modelling and information-theoretic approach used in the primary data analyses provided insight into the relative influence of important habitat characteristics, and enabled ranking of the predictive power of these. In particular, the generalised additive mixed models (GAMM) worked well to examine the community and population responses of native fauna, and gave insight into the non-linear relationships between fauna and habitat characteristics. Importantly, the GAMM plots enabled a range of ecological thresholds or ‘tipping points’ to be identified for fauna responses to specific habitat characteristics in remnant through to highly disturbed novel ecosystems. A range of responses across multiple responses and scales should therefore be used to assess and model habitat quality and quantify fauna responses in hybrid and novel ecosystems where they may rely on the novel habitat for persistence.

5.5 Future research directions

This study has investigated the response of native fauna to non-native plants as a case study and broader comparative analysis before developing conceptual frameworks to guide decision-making where native fauna are interacting with non-native plants. Conceptual models can be used as a practical tool to guide on-ground assessment (Lehtomäki & Moilanen 2013) or to evaluate different strategies (Frid et al. 2013) for conservation management. This present research has contributed to furthering knowledge of southern brown bandicoot ecology where it persists in blackberry habitat (Appendices 1 & 2). This information has already led to practical outcomes such as prioritising sites and on-ground works for restoration (A. Abley, pers. comm.). At a landscape scale, the research has allowed the Southern Brown Bandicoot Team for the Mount Lofty Ranges to develop and implement a decision-making tool to guide environmental practitioners in managing blackberry where it provides habitat for bandicoots (Appendix 3).

By adopting a combination of ecological, physiological and reproductive approaches, this current research has also identified a broad range of research questions that require further investigation. In particular, managing blackberry-dominated ecosystems for conservation would benefit from future research to identify:

- the total area of blackberry thickets within the Mount Lofty Ranges, and the distribution of extensive thickets (e.g. >200 m) in relation to native vegetation patches
- how a range of fauna species, including bush rats, brushtail possums, echidna and yellow-footed antechinus respond to blackberry habitat at a population level (in terms of fitness and productivity)
- whether small mammals in the Mount Lofty Ranges are experiencing an ‘extinction debt’ i.e. how the abundance and reproductive success of yellow-footed antechinus and southern brown bandicoots in this study compare with historical data
- effects of abiotic factors (including climate predictions) on small mammal communities, and population persistence for individual species, in novel ecosystems
- more robust baseline reference ranges for the haematology and biochemistry of southern brown bandicoots based on samples from populations throughout their distribution in Australia

- which native fauna species are dispersing seeds and fungal spores in novel ecosystems, the native and non-native species being dispersed, and the dispersal direction and distance
- whether native mammals promote mycorrhizal fungal-plant interactions in novel ecosystems by inoculating native fungal spores
- whether native mammal diggings increase the germination and recruitment of native plants in novel ecosystems
- whether blackberry acts as a nursery for native woodland plants in particular conditions and, if so, what the effect is on the germination and recruitment of native plants
- how blackberry could be managed in novel ecosystems to enhance the native regeneration of native plants and fungi promoted by small mammals
- the effect of different mechanical versus herbicide approaches on competitive interactions between native and non-native plant communities
- whether blackberry can be replaced (through regeneration or revegetation) by native species that afford the same cover and protection for native fauna
- patterns of gene flow in southern brown bandicoot populations in relation to the composition of blackberry and native vegetation patches in the Mount Lofty Ranges
- how native vegetation and fauna communities may respond to blackberry over the long term (e.g. next 100 years), including whether blackberry will further degrade ecosystems, act as a buffer for fauna persistence during climate change, or a combination in different ecosystem contexts.

It is unclear whether the long-term impact of fragmentation will be limited to species that are already in decline and have particular traits, or whether these threatened species are just the first to display fragmentation sensitivity in a broader trend towards biodiversity extinctions (Ewers & Didham 2006). Long term ecological studies can be indispensable for confirming links between fauna populations and landscape condition over time (Mosser et al. 2009), and would therefore provide insight into long-term trends within the native and novel ecosystems of the Mount Lofty Ranges.

The conceptual framework of native fauna–non-native plant assessments also raises many further questions for future research. In particular, it would be useful to extend the comparative analysis to include other native fauna responses such as individual movement patterns (e.g. the way in which home ranges change in response to novel ecosystems and broad-scale control of non-native plants), transients versus residents in population demographics, stress hormone levels (individual physiological fitness), and the effect of fauna on ecological processes in novel ecosystems (e.g. soil engineering, seed dispersal and pollination). These additional parameters would deepen our understanding of fauna responses at both the individual and population level, and therefore provide complementary insight for the development of more integrated conservation management strategies.

5.6 Concluding remarks on novel ecosystems: biodiversity sinks or buffers in a world of rapid ecological change?

Understanding the complex interactions between non-native plants and native fauna is essential if we are to successfully tackle the emerging conservation challenges of biological invasions (Hulme et al. 2013). The number of non-native plant species within native ecosystems continues to rise, and the need to understand the net effect of their impact on native fauna and flora is therefore becoming increasingly urgent for conservation management (Ellis et al. 1997). This is particularly important in novel ecosystems where the rapid broad-scale eradication of non-native plants may not only remove critical habitat for native fauna, but also slow down restoration through the removal of beneficial ecosystem processes (Rodriguez 2006; Schlaepfer et al. 2011; Hulme et al. 2013; Wortley et al. 2013). The development of successful conservation strategies requires an understanding of the impact of non-native species on native fauna diversity, abundance, fitness and productivity (Wright & Gribben 2008) in order to predict the consequences of weed control for native fauna populations. The findings from this present research highlight the importance of not making assumptions about the habitat quality of either native or novel ecosystems, and of investigating the net effect of habitat quality at the population and community level prior to planning management interventions. Only then can evidence-based ‘first, do no harm’ approaches (Sogge et al. 2008) of gradual adaptive management and ongoing review be tailored to the complex interactions of ecosystems.

Contrary to traditional views of novel ecosystems as degraded and inhospitable population sinks, this dissertation has found that habitat created by non-native plants in novel ecosystems can sometimes play a critical role in supporting meta-population productivity across fragmented landscapes. Novel ecosystems therefore have the potential to act as habitat buffers and linkages across landscapes that are fragmented and/or undergoing rapid changes such as broad-scale vegetation clearance or climate change. This opens the way forward to manage across multiple scales where novel ecosystems are a critical component within the landscape mosaic for native fauna populations that would otherwise become locally extinct.

Appendix 1

Conservation management outcomes from this research

Throughout the project there has been a strong partnership with the Government of South Australia's Southern Brown Bandicoot Recovery Team and local community groups including Trees for Life, Friends of Scott Creek Conservation Park, Friends of Mark Oliphant Conservation Park, Sturt Upper Reaches Landcare Group Inc., and Valley of the Bandicoots. These partnerships have enabled regular research updates to be presented and discussed with the Recovery Team and other groups, to collectively review the conservation implications of the research findings as they were reported, and to fine-tune the research focus to ensure it continued to target the most critical conservation issues for bandicoot and blackberry management.

The importance of this research project for bandicoot conservation in the Mount Lofty Ranges is summarised in the Southern Brown Bandicoot Recovery Plan 2010-2015:

> ***Threats – habitat degradation***
> *Data collected to date suggests that bandicoots occur at higher densities in large blackberry infestations within low density native vegetation than they do in naturally dense habitats (Packer unpubl. data, Snelling 2007). This may have significant implications for the long-term survival of bandicoots in habitats that would otherwise not support populations due to habitat fragmentation or degradation.*
>
> **Action 3.2. increase understanding of the role of blackberry as habitat**

Continue to support research to further investigate the effect of blackberry on habitat value for Southern Brown Bandicoot populations. Provide advice on broad-scale clearance of blackberry where it provides Southern Brown Bandicoot habitat within sparse native vegetation.

> ***Performance criteria****: Blackberry decision tool updated in response to research findings. Information provided to key landholders.*

One of the most significant and direct outcomes of the research has been the development of blackberry control guidelines by the Recovery Team in response to the research findings. The guidelines are summarised in a fact sheet on 'Blackberry Control in Bandicoot Country' (Appendix 2). The document aims to provide clear advice and a decision-making process for land managers on when and how to manage blackberry for bandicoot conservation. The second edition of the Blackberry Control in Bandicoot Country was finalised in June 2013 based on findings and recommendations from this research.

Government of South Australia
Department of Environment
and Natural Resources

Appendix 2

External Referee for Australian Geographic Sponsorship

Dr Joss Bentley
Threatened Fauna Ecologist
28 September 2010

1. Assessment of the significance of the proposed research

One of the key issues for recovery planning of the southern brown bandicoot is the extent to which blackberry provides critical habitat. Blackberry is a Weed of National Significance, and also a declared plant in the Mt Lofty Ranges, which requires that it be actively controlled. Based on some of Jasmin's preliminary findings, guidelines for blackberry control have already been amended.

Further, Jasmin's project currently provides the best known data set in Australia on seasonal changes in bandicoot population size, demography, and reproductive output. This will provide invaluable base-line data for interpreting population trends in the region's bandicoot program.

2. How will your organisation put the research outcomes into action to achieve long-term improvements for biodiversity conservation?

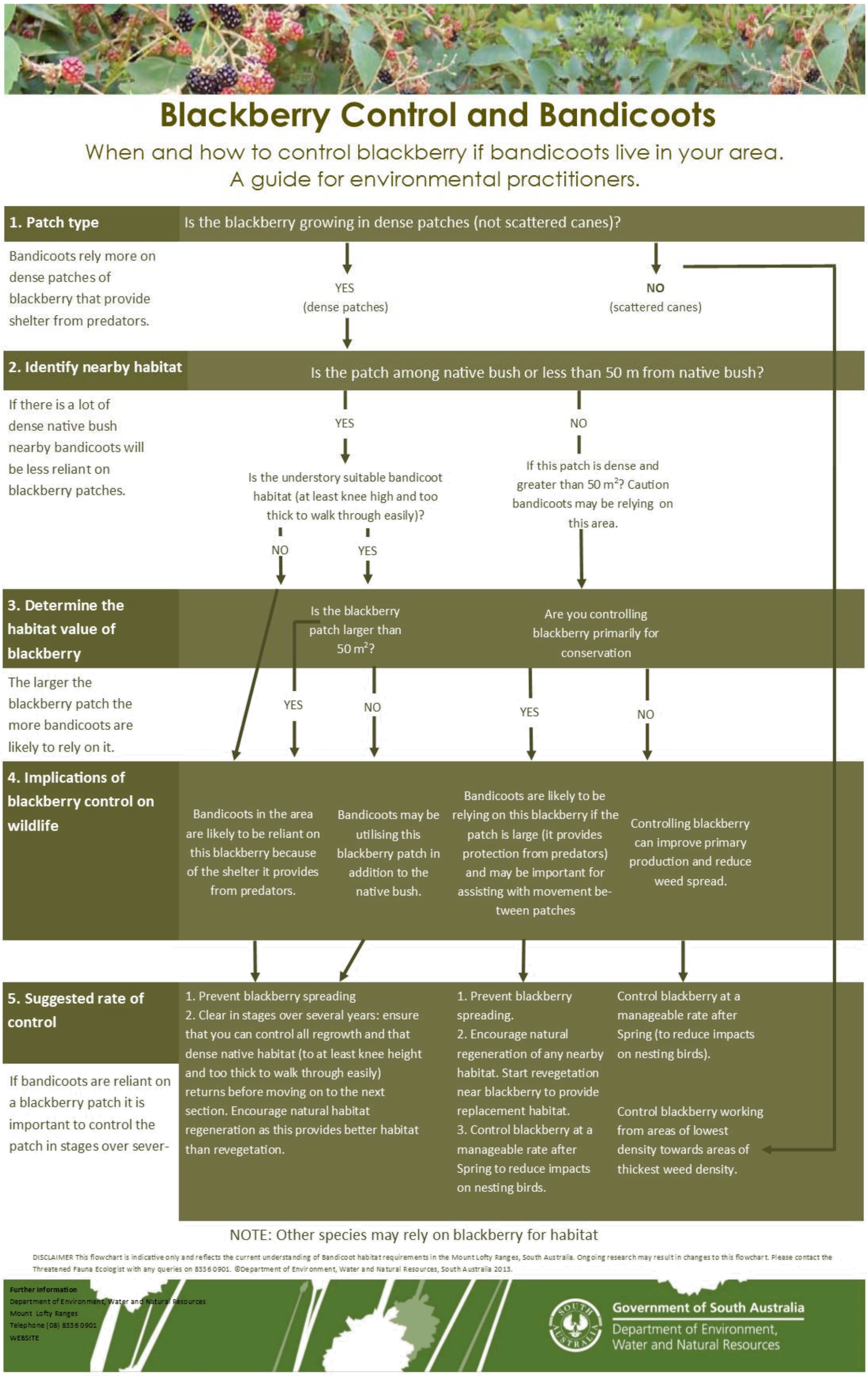
DENR is the lead agency for the conservation of biodiversity within South Australia. This research is very closely linked to the work of our group. The results of Jasmin's research will underpin the review of guidelines for the management of blackberry in areas with known bandicoot populations.

3. Assessment of the applicant's ability to deliver research outcomes

Jasmin has been an active member of the Recovery Team since its inception, and has a well developed knowledge of the issues relevant to this research project. Over the last couple of years she has developed a thorough and comprehensive research project, carefully targeted to address the critical research questions.

In addition to collecting comprehensive data on bandicoot habitat use, population parameters and habitat characteristics, through collaboration with veterinarians from the Zoo she is developing bandicoot health profiles which are likely to be provide critical insights into the factors influencing bandicoot fitness, information which is important to understanding the factors driving population dynamics. Although commonly used by ornithologists, this approach has rarely been used by mammalogists in Australia, and likely to prove particularly insightful. The preliminary findings of Jasmin's research are already proving useful.

Appendix 3



Blackberry Control and Bandicoots

When and how to control blackberry if bandicoots live in your area.
A guide for environmental practitioners.

1. Patch type

Bandicoots rely more on dense patches of blackberry that provide shelter from predators.

Is the blackberry growing in dense patches (not scattered canes)?

YES (dense patches)

NO (scattered canes)

2. Identify nearby habitat

If there is a lot of dense native bush nearby bandicoots will be less reliant on blackberry patches.

Is the patch among native bush or less than 50 m from native bush?

YES

Is the understory suitable bandicoot habitat (at least knee high and too thick to walk through easily)?

NO

YES

NO

If this patch is dense and greater than 50 m^2? Caution bandicoots may be relying on this area.

3. Determine the habitat value of blackberry

The larger the blackberry patch the more bandicoots are likely to rely on it.

Is the blackberry patch larger than 50 m^2?

YES

NO

Are you controlling blackberry primarily for conservation

YES

NO

4. Implications of blackberry control on wildlife

Bandicoots in the area are likely to be reliant on this blackberry because of the shelter it provides from predators.

Bandicoots may be utilising this blackberry patch in addition to the native bush.

Bandicoots are likely to be relying on this blackberry if the patch is large (it provides protection from predators) and may be important for assisting with movement between patches

Controlling blackberry can improve primary production and reduce weed spread.

5. Suggested rate of control

If bandicoots are reliant on a blackberry patch it is important to control the patch in stages over sever-

1. Prevent blackberry spreading
2. Clear in stages over several years: ensure that you can control all regrowth and that dense native habitat (to at least knee height and too thick to walk through easily) returns before moving on to the next section. Encourage natural habitat regeneration as this provides better habitat than revegetation.

1. Prevent blackberry spreading.
2. Encourage natural regeneration of any nearby habitat. Start revegetation near blackberry to provide replacement habitat.
3. Control blackberry at a manageable rate after Spring to reduce impacts on nesting birds.

Control blackberry at a manageable rate after Spring (to reduce impacts on nesting birds).

Control blackberry working from areas of lowest density towards areas of thickest weed density.

NOTE: Other species may rely on blackberry for habitat

DISCLAIMER This flowchart is indicative only and reflects the current understanding of Bandicoot habitat requirements in the Mount Lofty Ranges, South Australia. Ongoing research may result in changes to this flowchart. Please contact the Threatened Fauna Ecologist with any queries on 8336 0901. ©Department of Environment, Water and Natural Resources, South Australia 2013.

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List of Tables

List of Figures

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