Agricultural intensification and ecosystem function in a brigalow (*Acacia harpophylla*) landscape: implications for ecosystem services

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A thesis submitted for the award of Doctor of Philosophy

University of Southern Queensland

2007

ABSTRACT

Agricultural intensification, involving habitat fragmentation and modification, typically leads to a decline in biodiversity and ecosystem function. While most studies concentrate on remnant patches, the less intensively managed components of agricultural landscapes may also provide biodiversity values and ecosystem services. This study examines the contribution of different categories of land management to biodiversity and ecosystem function along a gradient of agricultural intensification. Differences within these land management categories are also examined. Research results are interpreted in the broad context of ecosystem services and their resilience in agro-ecosystems.

This research was conducted in the Brigalow Belt bioregion of southern Queensland near Dalby, Australia. Twenty-two small remnant brigalow (*Acacia harpophylla*) patches were selected and sampling sites established at the core and edge within the remnant and at the core and edge of an adjacent area of the agricultural matrix. Spatial information about remnant brigalow patch characteristics and attributes of the surrounding landscape were determined using aerial photographs and geographic information systems. Soil carbon concentration and the composition and diversity of plant and bird communities were used as ecological indicators. A combination of univariate and multivariate analysis methods was employed to compare indicators between core and edge across four distinct land management categories along a gradient of intensification. Spatial information was used to aggregate soil carbon data and to model the effects of landscape context on biotic communities.

Small, fragmented brigalow remnants contained higher levels of biodiversity and soil carbon and were compositionally distinct compared with the surrounding agricultural matrix of grassland and cropland. Soil carbon levels declined with increasing land use modification, with even the most sensitive (labile) carbon fractions showing little sign of recovery in naturally regenerating grasslands. Plant diversity also decreased with increasing land use intensity; however, cultivated areas reverted to semi-natural grassland assemblages following the cessation of regular tillage. Bird communities were predictably higher in the more structurally and floristically complex remnant brigalow but, unlike soil and plant indicators, showed little variation among matrix land management categories. Relationships for indicators measured across the vegetation-matrix boundary resembled a step function, with no detectable difference between core and edge in the same land management category. Plant and bird communities were influenced largely by landscape context variables, rather than measured local structural attributes of the vegetation.

Measured indicators in different land management categories along the intensification gradient showed distinct trends, with the nature of these relationships somewhat indicator-specific, particularly within the matrix. Different land management categories contained unique species assemblages, with all indicators higher in remnant brigalow. However, the significant contribution of secondary and regenerating grassland components of the agricultural matrix to biodiversity and ecosystem function are also highlighted. In particular, natural regeneration of plant communities in former arable lands, resulting in novel grassland ecosystems, suggests some degree of resilience in these systems and provides potential opportunities for enhancing biodiversity and ecosystem function. The observed similarity between core and edge for plants and soil carbon in both Brigalow and matrix suggests that land use boundaries are abrupt, with no detectable ecotone.

Results are discussed in the context of a state and transition model, enabling the conceptualization of changes between different land management categories caused by agricultural intensification and regeneration. The usefulness of the measured variables as potential indicators of ecosystem function in highly fragmented and modified agricultural landscapes is discussed. Inferences are made about the role that different landscape components play in maintaining overall ecosystem function and ecosystem services. A broader ecological approach to assessing biodiversity and ecosystem function in agro-ecosystems, that incorporates different land management categories and a range of ecological indicators, is recommended. In particular, the research suggests that the intrinsic value of the grassland components of the agricultural matrix for maintaining biodiversity and ecosystem function should be recognised and that natural remnant and semi-natural grassland components of the landscape should be maintained. This research is of particular value for balancing biodiversity conservation with production in brigalow landscapes and agro-ecosystems more generally.

CERTIFICATION OF DISSERTATION

I certify that the ideas, experimental work, results, analysis and conclusions reported in this dissertation are entirely my own effort, except where otherwise acknowledged. I also certify that the work is original and has not been previously submitted for any other award, except where otherwise acknowledged.

Signature of candidate	**Date**

ENDORSEMENT

Signature of supervisor/s	**Date**
	Date

ACKNOWLEDGEMENTS

I have many people to thank for their support throughout my PhD journey:

Thank you to my PhD supervisors Andy Le Brocque and Charlie Zammit. Thanks Charlie for your support, positive attitude, friendship and sage words during the initial and final stages and for making me think outside my comfort zone. Thanks Andy for willingly assuming the role of principal supervisor half way through and for making your time so freely available - your advice, patience and enthusiasm during thesis preparation are greatly appreciated.

Thank you to the past and present crew from the Land Use Research Centre and Australian Centre for Sustainable Catchments, who endured all of the tribulations and joys of the last few years with me. Special thanks to Fiona Morris, Simon Hill, David Grasby, Simon Attwood, Kellie Goodhew, Megan Brady, Pam Harris, Jayne Thorpe, Geoff Cockfield, Jerry Maroulis, Michelle Bouldin, Helen O'Callaghan, Marien Stark and Martine Maron. Thank you all for your support, stimulating conversations, inspiration and friendship. Special thanks to Kathryn Reardon-smith for her supportive words and field assistance in the early stages of the project, especially the 4am starts. I am grateful to Gareth Bramston, Jesse Soric, Pat McConnell, John Dearnaley, Andy Le Brocque, Melanie Bradley, Kate Reardon-Smith and Sarah Lewis for their enthusiastic field assistance.

Thanks to the technical and administrative staff from the Faculty of Sciences, who supported my research and were always willing to assist. These people include Debbie White, Pat McConnell, Chris DeByl, Phil Hallas and Oliver Kinder. Special thanks also to Ashley Plank for his statistical advice. Thanks to Ruth Hilton, Carla Hamilton and Christine Bartlett from the Office of Research and Higher Degrees for their assistance and administrative support during my candidature. Thanks to Alan House, Rod Fensham, Bruce Wilson, David Watson, Teresa Eyre, Scott Field, Armando Apan, Greg Ford and Bruce Lawrie for their guidance on technical matters at various stages of the research. Thanks to John Standley and other staff from Leslie Research Centre, Toowoomba for conducting all soil carbon analyses and for allowing me to use their drying ovens, soil grinders and other equipment.

Thanks to various editors for their insights and comments on draft papers and chapters, Andy Le Brocque, Charlie Zammit, Simon Lewis, Sarah Lewis, Martine Maron, Cliff Collard, Julia Playford, Anthony Whitbread, Joe Scanlan and Jerry Maroulis.

Thanks to the many landholders who allowed me to access their properties, despite adverse farming conditions and a turbulent political environment. Special thanks to Errol and Jewel Hartmann, Cliff Hartmann, Donny Chiverton, Kan and Denetta Achilles, Darryl and Suzette Handford, Neil and Andrea Radke, Robert and Pam Radke, Dalby Agricultural College, Royce Jensen, Peter and Tricia Morgan and to all others who granted me access to their properties.

Thanks and much love to my cherished partner and closest companion Sarah Lewis for moving to Queensland and her forbearance and unerring love during the past few years - I couldn't have finished this without you Gorgeous. Thanks also to all my fabulous friends in Toowoomba and further a field for your support, the fun trips away and for putting up with my vagueness and absence from far too many social occasions. Thanks to my family for their love and support from afar – knowing that you were thinking about me provided great comfort.

I am particularly grateful for the generous financial support provided by the Australian Research Council through an Australian Postgraduate Award (Industry partners: DNR&M and QPWS). Additional funding and support for the project was provided by the Land Use Research Centre/ Australian Centre for Sustainable Catchments and the Faculty of Sciences at the University of Southern Queensland.

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PUBLICATIONS

Collard, S.J. & Zammit, C. (2006). Effects of land use intensification on soil carbon and ecosystem services in Brigalow (*Acacia harpophylla*) landscapes of southeast Queensland, Australia. Agriculture, Ecosystems and Environment **117**:185-94.

Collard, S.J., Le Brocque, A. and Zammit, C. (in draft). Comparison of herbaceous plant communities along a gradient of agricultural intensification in a brigalow (*Acacia harpophylla*) landscape.

Collard, S.J., Le Brocque, A. and Zammit, C. (in draft). Bird community patterns in brigalow and adjacent matrix habitats and the influence of landscape context.

O'Farrell, P. and Collard, S. (2003). Ecosystem services: an examination of approaches to investigating ecosystem services in agricultural landscapes in South Africa and Australia. Proceedings of the International Rangelands Congress. Durban, South Africa, from 26 July – 1 August 2003.

PRESENTATIONS

Collard (2006). Landscape-scale carbon management in Brigalow (*Acacia harpophylla*) agro-ecosystems of southeast Queensland, Australia. Ecological Society of Australia conference Wellington –oral presentation.

Collard (2005). Ecosystem functioning across vegetation-production boundaries in Brigalow (*Acacia harpophylla*) in Southern Queensland. Ecological Society of Australia conference, Brisbane – oral presentation.

Collard (2004). Brigalow bird communities and ecosystem services in a fragmented agricultural landscape. Birds Australia Congress 2004, Crow's Nest.

Collard (2003). The contribution of bird communities to ecological services in agricultural lands surrounding Brigalow remnants. Ecological Society of Australia conference, Armidale – oral presentation.

Collard (2002). Brigalow vegetation and ecosystems services in southern Queensland – poster presentation. Ecological Society of Australia conference, Cairns.

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CHAPTER 1

GENERAL INTRODUCTION AND LITERATURE REVIEW

1.1 Overview

Ecological systems throughout the world continue to be altered and degraded at an increasingly rapid rate (Vitousek *et al.* 1997; Brown *et al.* 2001). Decline in the condition and extent of terrestrial natural systems is occurring primarily due to encroachment by humans for agriculture (Tilman *et al*. 2002; Foley *et al.* 2005). It is estimated that around one third of the earth's habitable surface is dominated by agriculture (Ormerod and Watkinson 2000). The consequent disturbance and fragmentation of ecological communities caused by agricultural intensification disrupts biophysical processes and ecological function from local to global scales, leading to the loss of biological diversity and land degradation (McLaughlin and Mineau 1995; Matson *et al.* 1997; Tscharntke *et al.* 2005), a reduction in the productive capacity and stability of affected landscapes (Naeem *et al*. 1994; Tilman 1996), and ultimately to the impoverishment of human communities (Palmer *et al.* 2004; Wright 2004; Diamond 2005).

As the extent and integrity of global ecosystems continue to diminish, their value to humans becomes increasingly apparent (Daily *et al*. 1997). The term 'ecosystem services' is now widely used to describe the many benefits to humans from functioning ecological systems (Millennium Ecosystem Assessment 2005). The existence of these services has been well documented (Holdren and Ehrlich 1974; Costanza *et al.* 1997; Daily *et al.* 1997; Cork *et al.* 2001). It is generally acknowledged that human populations are sustained by, and therefore dependent on, the services provided by functioning ecosystems (Daily *et al.* 1997). However, increasing human demand for food and fibre has created pressure to convert natural ecosystems and the services they provide to broad-scale production enterprises (Tilman *et al.* 2002). This has resulted in landscapes that are dominated by agriculture, with only small, fragmented areas of the original ecosystems preserved (Hobbs 1993). These 'remnant' areas, typically higher in biodiversity value than the surrounding agricultural landscape (Arnold *et al*. 1987; Tscharntke *et al*. 2002), may also be modified by local disturbances (e.g. grazing), changes to natural processes (e.g. exclusion of fire) or by management practices used in surrounding agricultural lands (McIntyre and Hobbs 1999). The extent to which this disturbance affects ecosystem services is much debated and remains poorly understood (Swift *et al*. 2004). The term agro-ecosystem is now commonly used to describe this type of semi-natural, human-modified landscape (Altieri 2002).

Agro-ecosystems usually contain elements of the original ecosystem in various states of modification, surrounded by a highly modified matrix of cultivated or grazing lands (Swift *et al*. 1996; McIntyre and Hobbs 1999; Altieri 2002). In this type of landscape mosaic, remnant ecosystem components such as native vegetation play an important role in maintaining biodiversity (Saunders 1989; Fischer and Lindenmayer 2002; Tscharntke *et al*. 2002) and in providing beneficial ecosystem services to agriculture-based rural communities (Bird 1992; Altieri 1999; Van Noordwijk *et al*. 2004). However, the role played by biodiversity in maintaining ecosystem function and services in these intensively managed agro-ecosystems is still largely unknown (Swift *et al*. 2004).

Furthermore, as the natural components of agro-ecosystems continue to diminish, the role of the agricultural matrix in maintaining biodiversity is increasingly being recognised (Kupfer *et al*. 2006; Martin *et al*. 2006). In particular, the composition and spatial configuration of the matrix of crops and grasslands in agro-ecosystems (i.e. landscape context) may provide intrinsic biodiversity value and influence the ability of some species to move through the landscape and successfully disperse and colonise new areas (Pearson 1993; Bender and Fahrig 2005; Brotons 2005). Managing this matrix to facilitate species' movement, by moderating the negative effects of isolation (Carroll *et al*. 2004), may have a significant influence on local biodiversity and wider-scale ecosystem function (Sisk *et al*. 1997; Lindenmayer *et al*. 2001). In a recent review, Kupfer *et al*. (2006) concluded that the mounting evidence for the influence of the matrix on biota in human-modified landscapes should prompt a shift in research efforts from patch-based examinations (e.g. patch area and distance metrics) to a model that recognises gradients of habitat quality in the matrix.

Extensive areas of the Brigalow Belt bioregion of southern Queensland have undergone recent broad-scale clearing of native vegetation (Wilson *et al.* 2000; Department of Natural Resources and Mines 2006) for intensive agriculture. Consequently, many of the brigalow (*Acacia harpophylla*) vegetation communities in this bioregion are now listed as endangered under State and Commonwealth Government legislation (Sattler and Williams 1999). However, little is known about the impacts of such land use intensification on the biodiversity of brigalow vegetation communities, and even less is known about how these changes may impact on the sustainable provision of ecosystem services to rural communities. In some long-established areas, the permanent or temporary retirement of ex-arable lands leads to the establishment of semi-natural grassland communities ('novel ecosystems' *sensu* Hobbs *et al*. 2006) that may be important for enhancing ecosystem biodiversity and resilience.

This thesis uses ecological indicators to compare biodiversity and ecosystem function at different points along a gradient of agricultural intensification in a highly modified agro-ecosystem in southern Queensland. Comparisons are made between different land uses (e.g. remnant woody vegetation, grassland and cropping) and between core and edge in the same land use. The research also examines the response of some of these indicators to landscape context. Research findings will be discussed in a broader context relating to resilience and ecosystem services in agricultural landscapes.

1.2 Agricultural intensification

Agricultural landscapes typically evolve along a gradient of increasing intensification caused by local modification and broader fragmentation of ecosystems (McIntyre and Hobbs 1999). These changes to vegetation and landscape in agricultural areas have led to changes in local and landscape-scale biodiversity and ecosystem function, by the conversion of one land use to another (e.g. brigalow to cropping), or by indirect factors such as fragmentation and resulting population isolation and edge effects (Saunders 1989; McIntyre and Hobbs 1999). In particular, habitat change, such as land use intensification for agriculture, is one of the most important drivers of biodiversity loss globally (Millennium Ecosystem Assessment 2005).

Clearing of native vegetation for agricultural production is often driven by increasing pressure on land managers to exploit natural capital and maximise the economic returns from their land (Dorricott *et al*. 1998; Boulter *et al*. 2000). These economic pressures invariably lead to an increase in the extent and intensity of land use practices, often resulting in the degradation of naturally occurring ecosystems and a reduction in the number of species (Catterall and Kingston 1993; Brown *et al*. 2000; Swift *et al*. 2004). In southern Australia, where widespread clearing of deep-rooted native vegetation for pasture and crops has led to severe, widespread and often irreversible degradation from salinity and erosion throughout large tracts of prime, temperate agricultural land (Diamond 2005; Beeton *et al*. 2006), with losses of productivity estimated to be worth billions of dollars (Commonwealth of Australia 2002). In these regions, large-scale and costly rehabilitation projects are currently underway to address biodiversity decline, salinity, erosion and poor water quality caused by agricultural management practices such as land clearing (Commonwealth of Australia 2002; Beeton *et al*. 2006).

Despite State and Commonwealth Government legislation to prevent ecosystem degradation and protect endangered ecological communities (e.g. Queensland *Vegetation Management Act 1999*; Commonwealth *Environmental Protection and Biodiversity Conservation Act 1999*), large areas of native vegetation in Australia continue to be degraded through inappropriate management practices, including continued land clearing and agricultural intensification (Yates and Hobbs 1997; Young *et al.* 1999). In recent years, the average annual rate of land clearing in Australia has exceeded 500,000 hectares (Australian Conservation Foundation 2001), with most taking place in Queensland and New South Wales. This annual clearing rate has been exceeded only by developing nations such as Brazil, Indonesia and Bolivia (UNFAO 2001). Such degrading management practices are particularly prevalent across large areas of southern inland Queensland (Hale and Lamb 2000; Wilson *et al*. 2000) and have been shown to adversely affect beneficial ecosystem processes and production values (Bird *et al*. 1992; McIntyre *et al*. 2000).

The broad-scale transformation of native vegetation to agricultural lands has been linked to local and regional declines in native biodiversity (Hobbs and Hopkins 1990; Saunders *et al*. 1991; Bennett 1997). Furthermore, land clearing, fire and grazing management and the spread of exotic species have significant effects on the functional integrity of native vegetation communities at local and regional scales (Fensham 1997; Lambeck 1997). These include changes to assemblages of plants and animals and associated ecological processes such as nutrient cycling (Prober *et al*. 2002), hydrological balance and biological invasions across a range of spatial scales (Hobbs 1989; Hobbs 1993). Possingham *et al.* (2002) proposed that preventing land-clearing in Queensland would be one of the most cost-efficient means of minimising Australia's ongoing loss of biodiversity. Indeed, from the start of 2007, State Government legislation in Queensland bans any further broad-scale clearing of native remnant vegetation.

1.3 Ecosystem services

1.3.1 Theoretical basis for the concept

It has long been recognised that functioning ecosystems are of great value to humanity (Ehrlich and Ehrlich 1970). However, the extent to which humans depend on ecosystems has become increasingly apparent as they diminish in extent and integrity (Ehrlich and Mooney 1983; Baskin 1997). In the past, humans have undervalued and assumed many of the free services provided by ecosystems. For example, the natural resources that provide the basis for many industries (e.g. agriculture and fisheries) have generally been in abundant supply and often considered to be inexhaustible and therefore taken for granted (Pimentel *et al*. 1997; Vitousek *et al*. 1997). However, the rapid depletion of renewable resources such as forests, fisheries and arable lands is forcing resource managers and consumers to reconsider the way these resources are harvested and managed, increasing the need for more sustainable management practices that reduce ecosystem degradation and increase resource use efficiency (Daily 2000).

The growing human demand for, and corresponding scarcity of natural resources, in combination with the widespread degradation of ecosystems, has forced ecologists to align existing theories and practices with contemporary ideologies and realities (Mooney and Ehrlich 1997; de Groot *et al.* 2002). The concept of ecosystem services is a salient example of this change in attitude and it is now being widely used in both scientific and public domains to describe the many benefits humans derive from natural, functioning ecosystems (Costanza *et al.* 1997; Daily *et al.* 1997; Millennium Ecosystem Assessment 2005). The emergence of this largely anthropocentric term reflects the increased need to publicly communicate the functional importance of natural systems, and to establish connections between natural assets, human needs and the economy. It is anticipated that raising public awareness of the functional importance of ecosystems to society will improve the long-term management of natural resources, including ecosystems (Daily *et al.* 1997).

Under this emerging paradigm, ecosystems are regarded as a form of natural capital that provides humans with a flow of benefits over time (Costanza *et al.* 1997; Van Noordwijk *et al.* 2004). These benefits are typically divided into ‘goods’ and ‘services’. Ecosystem goods have been defined by Daily *et al*. (1997) as “organisms and their parts and products that grow in the wild and are of direct benefit to humans”. Examples of ecosystem goods include commonly traded commodities such as seafood, timber and pharmaceuticals – these are traditionally considered ‘resources’ and can easily be assigned an economic value. In contrast, ecosystem services are defined as “the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfil human life" (Daily *et al.* 1997). These services have proven difficult to reliably quantify, and therefore to value in economic terms, resulting in ecosystem services being generally undervalued in the past (Costanza *et al.* 1997).

The use of the word 'services' implies that the functions carried out by ecosystems and their components, are of direct and tangible benefit to humans. Attempts have been made to identify and define these services. For example, Holdren and Ehrlich (1974) were among the first to articulate the numerous functions performed by ecosystems that are of benefit to humans. Among these services were the pollination of crops and native vegetation by insects, purification of air and water, maintenance of biodiversity, cycling and movement of nutrients, control of agricultural pests, micro-climatic stabilization and ecosystem self-regulation and maintenance. At a global scale, other services such as regulation of the gaseous composition of the atmosphere and its effects on climate become more important. In addition to these practical services, natural ecosystems also provide intangible benefits to humans such as intellectual and spiritual stimulation, pleasure from aesthetic beauty and future options (Kellert and Wilson 1993; Daily 1997).

The recent focus on ecosystem services (Costanza *et al*. 1997; Daily *et al*. 1997; Swift *et al*. 2004; Kremen 2005; Millennium Ecosystem Assessment 2005; Balvanera *et al*. 2006) reflects a recognition that beneficial services result from functioning ecosystems and that these services are inextricably linked to human well-being and the productive capacity and sustainability of human-modified landscapes (Francis 1989; Hendrix *et al.* 1990; Swift and Anderson 1993; Naaem *et al*. 1994). For example, Costanza *et al*. (1997) estimated that ecosystem goods such as fish stocks and ecosystem services such as biological control, soil formation and pollination contribute US $33 trillion to society per annum globally, a figure that far outweighs global gross national product. A similar method was used by Glanznig (1999), to derive an estimate of AU $1.3 billion for ecosystem services in Australia.

However, there is a lack of robust empirical evidence to underpin ecosystem services theory and its application in modified landscapes such as agro-ecosystems (Cork *et al*. 2001; Swift *et al*. 2004). In particular, the ecological basis for the quantification of ecosystem services remains poorly understood (Kremen 2005). Despite significant research on describing some ecosystem services both in Australia and overseas, it remains uncertain whether the services concept is useful in empirical ecological research and assessment (Swift *et al*. 2004). In particular, it is unclear whether the concept of ecosystem services provides more than heuristic value for better communicating societal dependence on ecological systems.

This lack of understanding may be attributed to the complexities associated with accurately modelling ecosystems and quantifying ecological function (Tscharntke *et al*. 2005). Of particular importance are the uncertainties surrounding relationships between biodiversity and ecosystem functioning and the assumed positive relationship between biodiversity and the persistence of ecosystem services (Swift *et al*. 2004; Kremen 2005; Fischer *et al*. 2006). Nevertheless, as ecosystem services diminish and thus become more valuable, natural resource managers are increasingly seeking to place values on these services. Inevitable questions are being asked about their ecological basis and the numbers and types of species required to maintain them (Daily *et al*. 1997). A meaningful method for measuring the value of ecosystem services is therefore needed, with strong supporting ecological science, so that impacts of human activities on ecosystem services can be explored and predicted (Cork *et al*. 2001). In particular, a better knowledge of the relationships between biodiversity and function at different spatial and temporal scales is crucial for our understanding of ecosystem services and their role in commodity production (e.g. agricultural) landscapes.

1.3.2 Ecosystem services in agro-ecosystems

In most agro-ecosystems only small areas of the native ecosystem remain in the landscape and these areas are usually modified by human land management practices (Altieri 1999; McIntyre and Hobbs 1999). However, there is growing evidence to support the functional role played by these fragmented natural or semi-natural landscape components in maintaining biodiversity and thus providing critical ecosystem services (Matson *et al*. 1997; Tscharntke *et al*. 2002; Fischer *et al*. 2006). For example, a number of studies have examined the direct benefits to production enterprises afforded by non-agricultural habitats in agro-ecosystems (see Altieri 1999). In particular, non-crop habitats interspersed among cropping areas provide a source of beneficial vertebrates (Fowler 1991), and invertebrates (Duelli 1999; Theis and Tscharntke 1999), help prevent soil erosion (Forman and Baudry 1984; Hobbs 1993), mitigate contamination of water by agricultural chemicals (Ryszkowski *et al*. 1999), filter water and reduce flooding (Daily 1997). More specifically, Thies and Tscharnke (1999) detected higher parasitism of rape pollen beetles by wasps in areas adjacent to field margins. Furthermore, Jones *et al*. (2005) described the pest control services and potential benefits to production made by some insectivorous bird species (Tremblay *et al*. 2001; Sekercioglu 2006).

Compared with major studies overseas (e.g. Costanza *et al.* 1997; Daily 1997), there has been relatively little quantitative research on agro-ecosystem services in Australia. Significant work has been conducted by Binning *et al*. (2001) examining ecosystem services in the Goulburn-Broken region of northern Victoria. This research provided a comprehensive inventory of natural assets of the region as the basis for investigating ecosystem services relevant to specific industries, and used this information to inform policy and natural resource management decisions in the area. The focus of their research was not to understand the ecological aspects, but rather to focus on quantifying the range of ecosystem services. In this sense, the work is more akin to regional development planning than ecological research. Oliver *et al*. (2005) have also made progress towards developing a set of biophysical indicators that relate to ecosystem services at a catchment or regional scale in New South Wales. A number of smaller case studies on ecosystem services are currently being carried out in different regions of Australia. For example, key research in the Atherton Tablelands and Brisbane Valley in Queensland, the Gwydir Valley and rangelands of NSW, and in the Blackwood catchment of Western Australia aim to understand ecological pathways for the provision of ecosystem services (Ecosystem services project 2004, accessed 6/7/2006). However, few published studies have addressed the issue of how these ecosystem services relate to biodiversity and ecosystem function at a local (management) scale in Australian agricultural landscapes.

1.3.3 Biodiversity, ecosystem function and agro-ecosystem services

The sustainable provision of ecosystem goods and services relies on the operation of complex interactions between a diverse array of biotic and abiotic ecosystem components (Daily 1997; Altieri 1999; Swift *et al*. 2004). Biodiversity is generated and maintained by natural ecosystem processes and its benefits are expressed in many of the goods and services provided by ecosystems (Tilman 1997). For example, biodiversity is a direct source of ecosystem goods, by supplying the genetic and biochemical resources that sustain human activities such as agriculture, fisheries and forestry (Daily *et al*. 1997). Many of the biochemical and biophysical processes in ecosystems, such as the stores and flows of energy, water and nutrients are dependent upon the assemblage of different species (biodiversity) in the ecosystem (Tilman and Downing 1994; Mooney *et al*. 1996). Human-induced changes to this biodiversity (e.g. through agricultural intensification) can alter ecosystem properties, potentially affecting ecosystem function and the goods and services that ecosystems provide to human communities (Hooper *et al*. 2005; Tscharntke *et al*. 2005).

Vitousek and Hooper (1994) proposed three possible relationships between plant diversity and ecosystem function, such as the rate of primary production (Figure 1.1). Curve 1 represents the "rivet" hypothesis (Lawton and Brown 1993) which implies that the more species there are in a system, the greater the ecological function and that any loss of species from a system affects its function. Hence a generalised linear (additive) relationship may be expected. Curve 2 shows the "redundancy" hypothesis (Lawton and Brown 1993), which suggests that some species may not contribute to the function of the system – that is, they are functionally redundant. This theory implies that the loss of some species does not affect function (i.e. the system is resilient to some species loss), but that if species loss exceeds a certain threshold, function is affected. Curve 3 suggests that the relationship is non-existent, with additional species (other than those already performing the function (e.g. decomposition)) having no effect (Vitousek and Hooper 1994). Based on an analysis of the available evidence at the time of publication, the asymptotic relationship represented by Curve 2 was deemed by the authors to be the most likely relationship, suggesting that ecosystem functions such as primary production may require a certain minimum level of biodiversity, but that the actual number of species required to maintain function (i.e. reach saturation point) may be quite small.

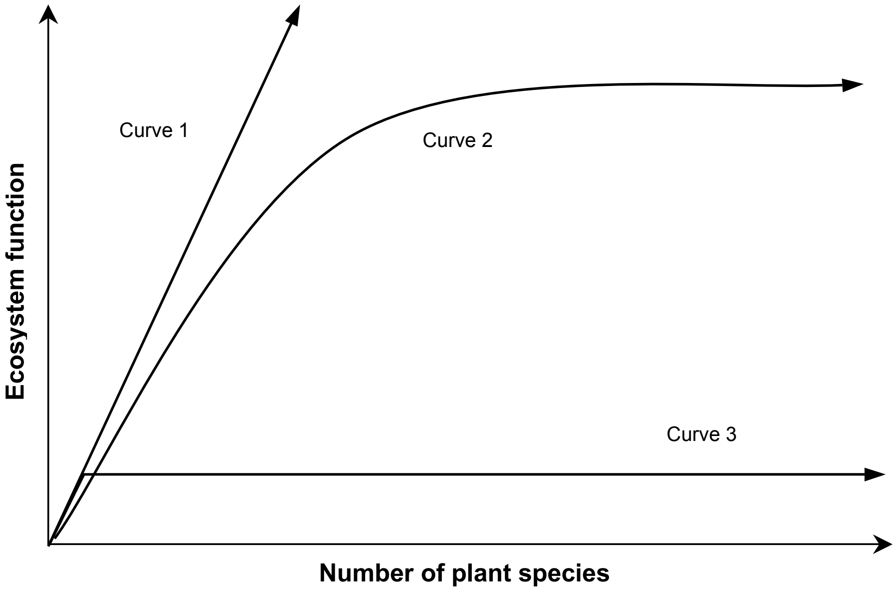

Figure 1.1. Possible relationships between biodiversity (as measured by the number of plant species) and ecosystem function (e.g. primary production) adapted from Vitousek and Hooper (1994). Curve 1 represents the 'rivet hypothesis', Curve 2 represents the 'redundancy hypothesis' and Curve 3 represents no relationship between biodiversity and function, with additional species having no effect on function.

A number of studies have used experimental approaches to test the relationships between biodiversity and function posited by Vitousek and Hooper (1994). Some of these studies appear to support the finding that functioning (as measured by plant primary production) increases with a greater number of species (Naeem *et al*. 1994; Tilman 1997). In particular, Bullock *et al*. (2001) showed that after 1 year of growth, hay yield was up to 60% higher in species rich (25-41 species) than species poor (6-17 species) plant communities. Others have shown high redundancy of species for ecosystem functions such as decomposition (Wardle *et al*. 2000) and insect parasitism (Rodriguez and Hawkins 2000). In a meta-analysis of research on the relationships between biodiversity and ecosystem processes, Balvanera *et al*. (2006) found clear evidence of a positive relationship between biodiversity and ecosystem function from studies that used primary productivity and nutrient cycling to reflect function.

However, various authors have been critical of the methods used and inferences made in studies that show a positive relationship between biodiversity and function (e.g. Grime 1997, Lawton *et al*. 1998). In particular, critics have pointed out that the controlled conditions under which these experiments were conducted and the small number of species used were not adequately representative of natural communities. More specifically, sampling effects, caused by uneven growth rates and competition between species, may have influenced niche assembly, particularly in the initial stages of growth (Huston 1997; Tilman *et al*. 2001). Interestingly, Swift *et al*. (2004) noted that the results of these controlled experiments may be more relevant in the managed components of agro-ecosystems than in natural systems where species have been intentionally assembled in a similar manner.

Adding to the uncertainty, Swift *et al*. (2004, pg 125) proposed that the “rules may change across spatial scales”. For example, various authors have postulated that the functional significance of biodiversity may become increasingly important to ecosystem functioning at larger spatial and temporal scales (Bond and Chase 2002; Bengtsson *et al*. 2003). This is because movement between local systems facilitates complimentary ecosystem interactions across spatial and temporal gradients (Loreau *et al*. 2003). In a review, Tscharntke *et al*. (2005)

concluded that there may be little empirical evidence to definitively substantiate links between local biodiversity and functioning, but that these relationships may operate at larger spatial and temporal scales, particularly in temporally and spatially dynamic agro-ecosystems.

A diverse array of species may also become more important when environmental change occurs (Vandermeer *et al*. 1998). This observation is particularly relevant when debating the significance of biodiversity in the face of perturbations such as agricultural intensification and global climate change. Such changing environmental circumstances may affect the ability of certain species and functional groups of species to maintain key functions (Swift *et al*. 2004). The capacity of a system to respond and recover from such disturbances is termed its ‘resilience’ (Holling 1973). Resilience has been linked to the diversity and community composition of ecosystems (Holling 1973; Walker 1995; Fischer *et al*. 2006) and may depend on the ability of species to recolonise from surrounding areas following such perturbations. Swift *et al*. (2004) proposed that resilience should be regarded as an ecosystem service, rather than as a ‘unitary ecosystem property’ because of its important role in maintaining ecosystems, including human communities.

There is mounting evidence of the important role played by biodiversity in maintaining essential ecosystem functions and hence, beneficial services and resilience in agro-ecosystems (Altieri 1999; Tscharntke *et al*. 2005). However, the numbers and types of species required to achieve this remain uncertain and continue to be a contentious area of scientific and political debate (Darwin 1872; Schulze and Mooney 1994; Grime 1997). Furthermore, the changes in land management that affect biodiversity in agro-ecosystems, are driven largely by community perceptions, which are in turn, influenced by social and economic imperatives (Frost 2000).

Some authors contend that the sustainable management of biological diversity and ecosystem services depends as much on society's ethical views as on facts (Barrett 1993). For example, different sectors of society confer different values on biodiversity depending on their cultural and religious belief systems (Nunes and van der Bergh 2001; Farber *et al*. 2002; Swift *et al*. 2004). These differing community values and their ultimate manifestation as changes in land management are often incompatible with the goals of maintaining high levels of biodiversity (Barrett 1993; Gardner and Stern 1996; Fairbrother 1998; Foley *et al*. 2005). In particular, management practices that lead to the modification and fragmentation of natural components of agro-ecosystems such as land clearing, grazing, pesticide and fertilizer application and the introduction of exotic species may adversely affect ecosystem function and services in agro-ecosystems (Hale and Lamb 2000). Although recognised as an important component in maintaining biodiversity and sustaining ecosystem services in agro-ecosystems, examination of these socio-economic perspectives will not form a part of the empirical research presented in this thesis.

While not explicitly focussed on measuring all aspects of ecosystem services, many indicators of ecosystem function also reflect the goods and services provided by ecosystems (Duelli and Obrist 2003). The research presented in this dissertation will therefore focus on indicators of biodiversity and ecosystem function, and their response to changes in the type and intensity of land management, rather than ecosystem service *per se*, The findings of these ecological assessments will be discussed in a broader ecosystem services context.

1.4 Indicators of biodiversity and ecosystem function

The lack of consensus on the fundamental relationships between biodiversity and ecosystem function in real landscapes, highlights the importance of selecting accurate and representative measures that describe ecosystem components and the links between them (Swift *et al*. 2004). Ecological indicators are widely used in this role as surrogate measures for ecosystem function and are, in turn, used to gauge the effects of 'stressors' on ecosystems (Andreasen *et al*. 2001) and the integrity and resilience of those ecosystems (Bouma 2002). Appropriate indicators of ecosystem function at a range of spatial scales and their links to biodiversity are required to further elucidate these often assumed relationships.

Biodiversity is usually quantified in terms of the number and relative abundance of species (i.e. particular genotypes) in a system (Daily *et al*. 1997b). However, some studies have emphasised the importance of considering other aspects of biodiversity such as community composition, functional groups and the relationships between species in space and time (Wardle *et al*. 2000; Swift *et al*. 2004). For example, Noss (1990) described biodiversity as a nested hierarchy of biological organisation, consisting of compositional, structural and functional attributes, operating at four levels of organisation: regional landscape; community-ecosystem; population-species; and genetic. Composition refers to species' populations, structure refers to the spatial distribution of species and function refers to the contribution of different species to ecosystem processes. This multi-faceted definition of biodiversity reflects the inherent complexity of ecosystems and the relationships between their biotic and abiotic components (Noss 1990).

In this thesis, biodiversity is referred to in its broader sense, encompassing the number and variety of species and the processes of which they are a part (Noss 1990; Loreau *et al*. 2001). Ecosystem function is regarded as an intrinsic ecosystem characteristic related to the set of conditions and processes under which an ecosystem maintains its integrity (Schultze and Mooney 1994). Changes in some aspects of biodiversity and ecosystem function may be partially represented by surrogate measures such as species richness, species diversity and community composition. Such ecological indicators are used in this study to compare aspects of biodiversity and ecosystem function between different agro-ecosystem components.

Other authors have emphasised the importance of considering different ‘functional groups’ in maintaining ecosystem function (Elmqvist *et al*. 2003; Swift *et al*. 2004). In particular, Bengtsson (1998) argued the importance of understanding the linkages between key species or functional groups and ecosystem function, rather than focusing on species diversity. Species are typically classified into functional groups based on their taxonomic, trophic or behavioural characteristics and their effects on specific ecosystem-level processes (Bengtsson 1998) with the classification system (e.g. the degree of sub-division of the species assemblage) dependent on the specific function being assessed. Swift *et al*. (2004) suggested that the total diversity required for a certain function depends on the number of functions that are recognised and the degree of overlap in functional groups.

Key species or functional groups of organisms in ecosystems show differences in life history attributes and may respond in different ways to environmental changes such as intensification in agro-ecosystems. The role of these different species or groups in maintaining ecosystem function may be different and some may be more resilient to change than others (Swift *et al*. 2004). Therefore, assessing the diversity of species between and within functional groups may provide useful information on the resilience (ability to recover following disturbance) of ecosystems (Walker 1995; Yachi and Loreau 1999). Diversity of species within different functional groups may improve the likelihood of maintaining specific functions in an ecosystem, particularly if changes to the system occur. Griffin (1972) provided evidence that different bacteria or fungi in the soil perform the same enzymatic function under different conditions of moisture stress or pH. Plants may play a similar functional role in different seasons under changing climatic or edaphic conditions (Walker *et al*. 1999).

The use of indicators to assess ecosystem function relies on the ability of the selected indicators to reflect the conditions of not only the ecosystem component being assessed, but also those organisms and processes associated with it (e.g. predators, prey, symbionts and so on). Different ecological indicators reflect different aspects of biodiversity and ecosystem function (Dale and Beyeler 2001; Duelli and Obrist 2003). It would be unrealistic to expect that individual measures would represent function for the entire ecosystem and all of its interacting components (Freudenberger and Harvey 2003). Therefore, more than one indicator is needed to reflect different aspects of ecosystem function at different trophic levels and spatial scales (Duelli 1997; Andreasen *et al*. 2001) and careful selection of a combination of ecological indicators can be useful in reflecting an overall level of ecosystem function (Duelli 1997; Lambeck 1997). Furthermore, research on the use of indicators has found that a relatively small number of indicators may be sufficient to represent overall function in some systems (Walker and Reuter 1996; Dale and Beyeler 2001).

Indicators are also widely used to assess the condition of, and key threats to biodiversity at broader spatial scales (Saunders *et al*. 1998). Surrogate measures such as total areal coverage of different native vegetation communities are commonly used to indicate ecosystem function (Bastin *et al*. 2002). Such broad-scale indicators of function clearly provide important information on large scale ecological processes but, in general, are of limited use for land managers at a local scale. In particular, measurements of indicators at this coarse level alone are not likely to detect smaller-scale processes and changes influencing biotic communities and ecosystem function, such as the effects of habitat complexity or patch size (Nagendra and Gadgil 1999; Ferrier 2002). Hence, accurate, multi-scaled indicators of ecosystem function are needed when considering biodiversity and ecosystem function in agro-ecosystems (Duelli 1997; Andreasen *et al*. 2001).

Various authors have reviewed the use of indicators in agro-ecosystems and suggested possible combinations that best represent different structural, functional and compositional aspects of these systems (Noss 1990; Dale and Beyeler 2001). For example Duelli (1997) suggested combining site-specific biodiversity measures (e.g invertebrates) with assessments of habitat diversity and heterogeneity using a set of different approaches, methods and relative measures. Other Australian studies also suggest a range of local- and landscape-scale indicators (see Walker and Reuter 1996; Parkes *et al*. 2003; Oliver 2004; Williams 2004). Common across all of these approaches is the combination of indicators that reflect differences in land management at different spatial scales (Andreasen *et al*. 2001). In this dissertation, indicators were selected to represent biodiversity and ecosystem function in different land uses along a gradient of agricultural intensification and regeneration.

1.5 Effects of agricultural intensification on biodiversity

Modern agricultural ecosystems, such as those of the Brigalow Belt bioregion in southern Queensland, typically evolve along a gradient of increasing land use intensification and structural simplification, from natural vegetation, through pastoralism, to an intensively managed mosaic of monocultures (Matson *et al*. 1997; Ryszkowski and Jankowiak 2002). The biotic community at any particular location in an agro-ecosystem depends on the current and historical intensity and duration of management practices (modification) and on the amount and spatial configuration of different land uses in the surrounding landscape (fragmentation) (Miller *et al*. 1997; McIntyre and Hobbs 1999; Lunt and Spooner 2005).

Agricultural intensification has been shown in a number of different ecosystems to be accompanied by a concomitant decrease in native species diversity and by a change in community composition (McLaughlin and Mineau 1995; McIntyre and Martin 2001; Fedoroff *et al*. 2005). These changes may be influenced by the duration and intensity of local-scale modifications such as vegetation clearing and continual soil disturbance (Duelli 1997; Chalmers *et al*. 2005). Changes may also be caused by more subtle disturbances at vegetation patch edges such as competition by weeds and exposure to increased temperatures and light levels (Forman 1995; Fox *et al*. 1997; Ross 2005).

Ecological communities may also be affected by broader-scale processes such as habitat fragmentation and consequent population isolation and by simplification and homogenisation of the surrounding landscape (Southwood and Way 1970;

Saunders *et al*. 1991; Wagner *et al*. 2000; Fahrig 2003; Tscharntke *et al*. 2005). In agro-ecosystems such as those of the southern Brigalow Belt bioregion, agricultural intensification may affect not only within-patch ecosystem interactions (alpha-diversity), but also between-patch differences (beta-diversity) and ecological communities at the landscape scale (gamma-diversity) (Matson *et al*. 1997). Efforts to conserve biodiversity and to maintain ecosystem services in agro-ecosystems must therefore consider ecological communities and the processes affecting them, at a range of spatial scales (Baudry *et al*. 2000).

1.5.1 Habitat modification

At a local scale, modification of existing ecosystems and transformation to grazing and cropping lands (intensification of management) can cause changes in community composition, significant reductions in the number of species (through local extinctions) and an overall decline in ecosystem function (Matson *et al*. 1997). Studies have also shown that modified habitats, such as grassland and cropland, contain lower species richness compared with more structurally diverse native woody vegetation (Arnold *et al*. 1987; Martin and Catterall 2001; Laiolo 2005; Woodhouse *et al*. 2005; Martin *et al*. 2006). Changes in biological communities through disturbances such as agricultural intensification and loss of biodiversity may have an adverse impact on ecosystem function by affecting soil processes, nutrient cycling and trophic interactions at local (i.e. paddock) and landscape scales (Hobbs and Huenneke 1992; Hobbs 1993; Tilman 1997). Hence, species assemblages in agro-ecosystems are shaped by a combination of natural perturbations, such as climatic fluctuations and fire, and by human–induced changes to the abiotic environment, such as those made by land managers through the direct and indirect regulation of populations of some species (e.g. weeds, crops, pests and diseases) (Swift *et al*. 2004).

1.5.2 Habitat fragmentation

Processes that operate at larger scales may also influence, and even override, local-scale effects on species (Swift *et al*. 2004). In particular, the spatial patterning of landscape elements may affect biophysical ecosystem processes such as the movement of species (Lambeck 1997; Freudenberger 1999) and thus, influence ecological function. For example, the fragmentation of vegetation remnants has a significant effect on the occupancy of plant (Weibull *et al*. 2003; Ross 2005) and animal species (Opdam *et al*. 1985; Barrett *et al*. 1994). The number, size and condition of native vegetation patches in the landscape mosaic, combined with their positioning in relation to each other (spatial configuration), may also influence many of the ecosystem processes (e.g. rising groundwater and soil erosion) that operate in agro-ecosystems (Hobbs 1993).

Patches of remnant native vegetation in agro-ecosystems are typically small, highly fragmented and isolated from other similar patches by large expanses of agricultural land (Andren 1994; Forman 1995). The effects of this isolation, combined with an overall reduction in the extent of original habitat, invariably leads to changes in animal and plant communities inhabiting the remaining, fragmented ecosystems (Saunders *et al*. 1991; Barrett *et al*. 1994; Watson *et al*. 2000; Major *et al*. 2001). Many studies have assessed the effects of this habitat fragmentation on animal communities (e.g. van Dorp and Opdam 1987; Saunders 1989; Bennett and Ford 1997; Ludwig *et al*. 1997). Most of these studies use mobile, higher order vertebrates such as birds, combined with landscape metrics such as area, shape, proximity to other patches and degree of connectivity between patches to determine the effects of landscape fragmentation on biodiversity (Andren 1994; Forman 1995). Combined, these measurements are useful for reflecting changes to ecosystem function at the landscape scale (Saunders *et al*. 1991).

Despite their small size and modified condition, fragmented patches of native vegetation are regarded by ecologists as functionally important components of the agricultural landscape because they provide an important refuge for biodiversity in an otherwise ecologically degraded and structurally simplified landscape (Barrett *et al*. 1994; Tscharntke *et al*. 2002). Fischer and Lindenmayer (2002) found that 75% of all bird species predicted to be found in a fragmented landscape in south eastern Australia, were detected in remnant patches of between 0.4 and 15.6 ha. Even single scattered trees provide important habitat for a range of higher and lower-order organisms in agricultural landscapes (Gibbons and Boak 2002). However, as patches of native habitat become smaller, through broad-scale fragmentation, they may also become increasingly exposed to disturbances from surrounding areas (Forman 1995; Martin *et al*. 2006).

1.5.3 Edge effects

In small, highly fragmented patches of native vegetation, typical of those in Australian agro-ecosystems, biotic communities may be adversely affected by structural and micro-climatic changes associated with fragmentation such as the creation of artificial patch edges (Lovejoy *et al*. 1986; Saunders *et al*. 1991; Murcia 1995; Stratford and Stouffer 1999). In agro-ecosystems, these habitat boundaries are typically abrupt (Dauber and Wolters 2004), and habitat edges exhibit environmental gradients and differences in biotic communities (Duelli 1997; Fox *et al*. 1997; Ries and Sisk 2004; Ross 2005).

An understanding of the biophysical processes at habitat edges is particularly important in agro-ecosystems because of the small size and high edge to area ratio of the remnant vegetation patches in these landscapes (Fagan *et al*. 1999). As patches of vegetation reduce in size, external disturbances are more likely to affect a greater proportion of the patch as the perimeter: area ratio increases and core area diminishes with size and linearity (Forman 1995). Edge disturbances in agro-ecosystems may include changes in microclimate such as exposure to wind and higher levels of solar radiation (Matlack 1993), competition from dispersive species (e.g. weed or pest species) from the surrounding matrix (Murcia 1995) or fertiliser runoff and herbicide/ pesticide drift (Kleijn and Snoeijing 1997; Boutin and Jobin 1998). Furthermore, the edge influence may vary according to the shape of the patch, the nature of the edge (Forman 1995) and the ability of the new species to colonise and compete with existing species (Murcia 1995). In small linear strips of vegetation, typical of intensive agricultural landscapes, this can have a significant impact on the overall integrity and species diversity of a patch.

Such edge effects may result in semi-natural biotic communities, consisting of some species that existed prior to fragmentation, combined with a new assemblage of disturbance-tolerant species from the surrounding landscape (Murcia 1995). Habitat edges that are adjacent to intensively farmed fields have a higher prevalence of introduced and/ or weedy species than edges adjacent to less intensively managed fields (Fox *et al*. 1997; Boutin and Jobin 1998). Sensitive species along habitat edges may also be displaced by ubiquitous generalist species that may be more tolerant to disturbance or able to use resources from the surrounding agricultural landscape (the matrix) to complement or substitute for resources from natural habitats (Grey *et al*. 1998; Luck *et al*. 1999; Norton *et al*. 2000; Piper and Catterall 2004). If patches are too small to maintain core habitat for some species, these species may become locally extinct, leading to the biotic homogenisation seen in some agro-ecosystems (McKinney and Lockwood 1999).

Edge responses vary for different indicators according to the nature of the edge and the type of response variable. Stronger edge responses are typically displayed at hard edges with high contrast between land uses, compared with soft (low contrast) edges (Reis and Sisk 2004). Three theoretical relationships based on empirically-derived response of different indicators across a range of different edge types were proposed by Reis and Sisk (2004). These included; 1) a neutral response (null model in Figure 1.2), showing no difference across patch edges, 2) a transitional response, where the steepness of the curve may vary according to the nature of the edge, or 3) a positive response, where levels of intermediate disturbance at the patch edge may enhance biological activity (Figure 1.2).

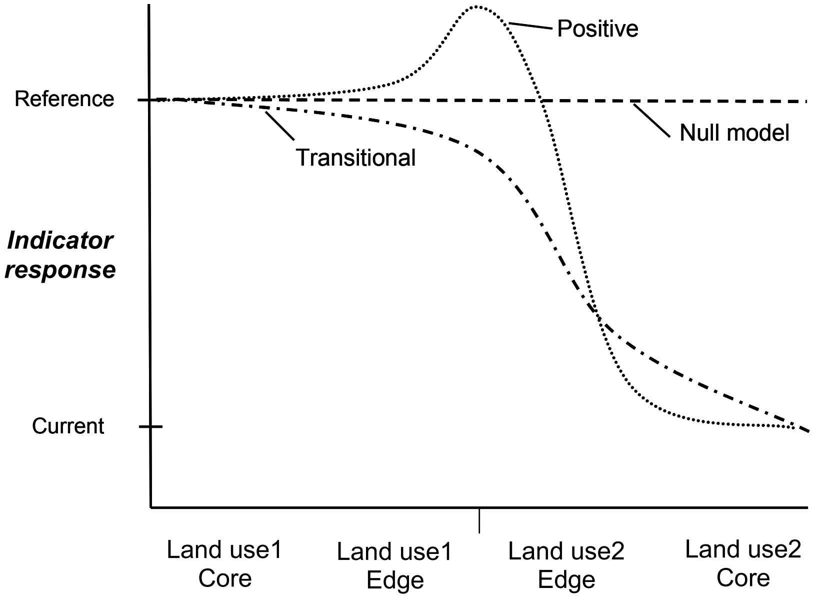

Figure 1.2. Responses of indicators across land use edges, based on the positive, transitional and null models proposed by Ries and Sisk (2004).

Many ecological studies have shown patterns of increased species richness at both natural and artificial (human-made) habitat edges (Angelstam 1992; Risser 1995; Fox *et al.* 1997). These 'ecotones' often contain higher species diversity than either of the two adjacent habitats because of the composite nature of the species assemblage (Angelstam 1992). Ecological theory suggests that some ecosystems maintain higher species richness under intermediate levels of disturbance (Connell 1978) such as at habitat edges (Forman 1995). However, species assemblages in the small and highly disturbed remnant patches in agro-ecosystems may also be affected by processes at larger scales such as declines in population viability caused by isolation and biotic homogenisation (McKinney and Lockwood 1999).

1.5.4 Matrix effects and landscape context

Until recently, island biogeography and metapopulation models, particularly in relation to patch size and distance to source populations, have been the dominant theories used to explain extinction and colonisation in fragmented agricultural landscapes (MacArthur and Wilson 1967; Hanski and Gilpin 1991). Under these traditional theories, fragmented patches of native vegetation have been regarded as discrete islands, surrounded by an inhospitable matrix of homogeneous farmland that is considered of little or no value for biodiversity conservation (MacArthur and Wilson 1967). However, more recently, the importance of the composition and configuration of other landscape components (e.g. grassland and cultivation in the surrounding agricultural landscape (i.e. 'the matrix')) are increasingly being recognised (Dauber *et al*. 2003; Kupfer *et al*. 2006). Ecologists are now using a more encompassing 'patch-corridor-matrix' or 'landscape mosaic' model (Forman and Godron 1981; Forman 1995) as the basis for examining biodiversity and ecosystem function in agricultural landscapes.

In agro-ecosystems, the matrix can be defined as the portion of the landscape that has, at some point in time, undergone intense anthropogenic perturbation such as clearing of the original vegetation (Ricketts 2001; Antongiovanni and Metzger 2005). In highly fragmented landscapes, such as those of the Brigalow Belt bioregion, remnant patches of vegetation comprise a small proportion of the overall landscape cover and are surrounded by a disproportionate area of matrix habitat. In these landscapes, the predominant agricultural matrix is typically heterogeneous, consisting of a variety of land uses, including native and improved grazing lands and crops in continuous rotation (Davies *et al*. 2001).

Recent studies in fragmented terrestrial environments such as agro-ecosystems, have shown that as natural ecosystems continue to diminish in extent and integrity, the composition and spatial configuration of the surrounding agricultural matrix may become more important factors influencing biodiversity conservation and the local occurrence of some species (Pearson 1993; Sisk *et al*. 1997; Bennett *et al*. 2004; Brotons 2005). In particular, the spatio-temporal characteristics of the surrounding matrix ('landscape context') may significantly influence the survival of some species (Fahrig 2001; Dauber *et al*. 2003; Kupfer *et al*. 2006).

Research on the effects of landscape context has revealed that biotic communities may be affected by a combination of local-scale habitat patch characteristics (e.g. habitat structural diversity, patch size) and by the nature and management of the surrounding landscape matrix (Mazerolle and Villard 1999; Fahrig 2001; Westphal *et al*. 2003; Yamaura *et al*. 2005). Some studies have shown that local-scale habitat factors have a strong influence on biotic communities (Watson *et al*. 2000; Major *et al*. 2001; Herzog and Kessler 2006). Other studies have shown that these communities may be affected by factors at a range of different spatial scales (Pearson 1993; Bennett *et al*. 2004; Martin *et al.* 2006). Furthermore, landscape context has been shown to moderate the negative effects of habitat isolation (Carroll *et al*. 2004), affecting both the composition of the species assemblage (Sisk *et al*. 1997; Lindenmayer *et al*. 2001), and rates of dispersal and patch colonisation (Bender and Fahrig 2005; Tscharntke *et al*. 2005). In a recent review, Kupfer *et al*. (2006) concluded that the mounting evidence for the influence of the matrix on biota in human-modified landscapes should prompt a shift in research efforts from patch-based examinations (e.g. patch area and distance metrics) to a landscape mosaic model that recognises the importance of habitat gradients in the matrix.

The majority of landscape ecological studies in Australian agricultural landscapes have been confined to fragmented patches of relatively undisturbed, pre-European native vegetation, with the surrounding matrix of crops and grassland considered a hostile environment for native biodiversity (e.g. Saunders 1989; Barrett *et al*. 1994; Freudenberger and Brooker 2004). Comparatively few studies have examined the predominant matrix of cleared and disturbed cropping and grazing lands, particularly in brigalow agro-ecosystems. Studies that examine the matrix focus mainly on plant community responses to grazing in native grasslands and grassy woodlands (e.g. Tremont 1994; Lunt 1997; Fensham 1998; McIntyre and Martin 2001; McIntyre and Martin 2002). Only a few studies have considered the more intensively managed cropping components of the matrix and their contribution to agricultural biodiversity (McIntyre and Martin 2001; Wong 2004; Chalmers *et al*. 2005; McIntyre *et al*. 2005; Martin *et al*. 2006).

1.6 Research aims and questions

This dissertation examines indicators of biodiversity and ecosystem function in both the remnant and matrix components of a highly fragmented brigalow landscape, and represents a novel approach to assessing the ecological response of brigalow communities to the combined effects of modification and fragmentation. More specifically, the research compares ecological indicators at the core and edge of different land uses at different points along a gradient of increasing agricultural intensification.

The broad research questions relating to these comparisons are:

- What contributions do different land uses along a gradient of agricultural intensification, make to biodiversity and ecosystem function?
- Are there detectable differences in biodiversity and ecosystem function between land use core and edge?
- Does the composition and configuration of the surrounding landscape (landscape context) influence locally-measured biodiversity and ecosystem function?

A range of indicators was selected to reflect ecological function in different land uses. Soil carbon reflects the functional importance of soils in ecological and agricultural systems (Daily *et al*. 1997). Measures of plant community structure and composition were used to link above ground processes with soil function and to provide information about habitat value for other organisms (e.g. birds). Bird communities were examined because of their spatial mobility and hence, their potential as predictors of broader-scale landscape intensification. All measured variables were linked to information on the spatial pattern and configuration of different land management types in the study landscape.

The experimental research aims to test the following hypotheses in a fragmented brigalow landscape using the indicators described above:

1. Avian and floristic community assemblages and ecosystem function differ among land uses along an agricultural intensification gradient;
2. Floristic community assemblages and ecosystem function are different at edge and core in the same land use;
3. Local habitat factors, have greater influence on avian and floristic community assemblages than landscape spatial factors such as fragmentation and context.

Research findings will be discussed within a broader context pertaining to biodiversity, ecosystem function and the provision of ecosystem services in agro-ecosystems.

1.7 Thesis overview

To test these hypotheses, soil carbon, plant communities and bird communities were sampled in a range of different land uses from remnant native vegetation to intensive dryland cropping. Chapter 2 describes the general characteristics of the study area, provides details of the specific study sites used for field monitoring and describes the general experimental design principles and analysis procedures used.

The effects of different levels of modification were tested for each indicator. Edge effects were tested only for soil carbon and plants and the effects of landscape context were tested only for plant and bird communities (Table 1.1).

Table 1.1. Hypotheses tested for each measured indicator

Indicator	Modification	Edge effect	Context/ fragmentation
Soil Carbon (Chapter 3)	✓	✓	
Plant diversity (Chapter 4)	✓	✓	✓
Bird diversity (Chapter 5)	✓		✓

Soil carbon levels between the core and edge and across different land uses are compared in Chapter 3. Instead of testing for the effects of landscape context on carbon levels, this chapter uses locally-derived measures of soil carbon and aggregates these to wider scales based on concentrations in individual land uses. A novel method for modelling soil carbon at local and broader scales is proposed (Collard and Zammit 2006). There are small differences in content and methodology between the chapter in this dissertation and the published manuscript.

Herbaceous plant composition, richness and structure are compared at core and edge in the same land use and between different land uses in Chapter 4. The effects of landscape context on plant communities in remnant vegetation and in the adjacent agricultural matrix are also tested. Chapter 5 compares bird richness, diversity and community composition across different land uses and tests for the effects of habitat structure and landscape context on locally sampled bird communities. Chapters 3, 4 and 5 are written as expanded manuscripts that have either been published or are being prepared for publication. Hence there is some repetition of background information in the introduction and methods sections of these chapters.

Chapter 6 draws out the main trends and differences between the measured indicators in each of the different land uses from the research presented in earlier chapters. This final chapter provides further critical analysis of the empirical data, interprets the key research findings and discusses the significance of these finding in a broader ecosystem services context. In addition, this chapter provides recommendations on the potential future management of biodiversity and ecosystem function in the study landscape.

CHAPTER 2

GENERAL METHODS AND LANDSCAPE INFORMATION

"I love trees more than anybody does, but the brigalow is a type of tree that nobody loves. You can't mill it, you can't use it as firewood, it's just useless rubbish" (Sir Joh Bjelke-Petersen, Premier of Queensland 1968-1987 (an oral history for the National Library of Australia – 2001)).

2.1 Description of study area

2.1.1 The Brigalow Belt bioregion of Queensland

The Brigalow Belt bioregion covers 36 400 000 hectares of eastern inland and coastal Queensland (Young *et al*. 1999), stretching from Narrabri in New South Wales in the south (30°30'S), to near Collinsville, Queensland (20° 30'S) in the north (Nix 1994) (Figure 2.2). The bioregion is broadly bisected into northern and southern sections and is divided into 36 sub-regions or provinces based on landform and vegetation type (Morgan and Terrey 1990). These provinces reflect major regional differences in physical and ecological processes (Davie *et al*. 1994) and are characterised by a variety of vegetation communities. Each province is further divided into regional ecosystem (RE) categories, defined as "a vegetation community in a bioregion that is consistently associated with a particular combination of geology, landform and soil" (Sattler and Williams 1999).

Prior to European settlement, a diverse range of vegetation communities (regional ecosystems), including eucalypt forest and woodland, grassland, dry rainforest and cypress pine woodland, existed throughout the Brigalow Belt bioregion (Sattler and Williams 1999). Plant communities consisting of the tree species *Acacia harpophylla* (brigalow) have a discontinuous distribution across approximately six million hectares of the bioregion (Johnson 1980).

2.1.2 Brigalow vegetation communities and biology

Brigalow, a legume, is classified in the Microneurae group of the Racosperma section Pleurinervia (Pedley 1986). This unique group grows predominantly in heavy-textured, cracking-clay soils typical of those in the lower lying areas of the Brigalow Belt bioregion (Isbell 1962). Brigalow is a native of Queensland and New South Wales and often grows in association with other tree and shrub species such as eucalypts (e.g. *Eucalyptus populnea*), Belah (*Casuarina cristata*), Wilga (*Geijera parviflora*) and a range of softwood scrub (dry rainforest) species in southern Queensland (Johnson 1964; Young *et al*. 1999). In the southern parts of the bioregion, brigalow vegetation associations, particularly those with softwood scrub elements are usually not exposed to fire under natural conditions (Bailey 1984).

The reproductive strategy of brigalow differs from many acacia species. For example, flowering and production of fruiting bodies (seed pods) occurs only infrequently in response to favourable seasonal conditions and soil water availability (Johnson 1964; Nix 1994). While most acacia species have hard seeds that remain dormant in the soil for long periods, brigalow produces seeds with a soft coat that germinate immediately following shedding. Brigalow plants also have an extensive system of starchy lateral roots which have the ability to develop adventitious buds if damage is caused to aerial parts or roots. Consequently, early tree clearing activities in the region such as felling, ringbarking and pulling often induced a massive suckering response, rendering large tracts of land unusable for production (Johnson 1964).

2.1.3 Development history and regulation

Much of the recent vegetation clearing in Australia has occurred across extensive areas of the Brigalow Belt bioregion (Bailey 1984; Fensham *et al*. 1998). The deep fertile soils of the southern section of this bioregion are among the best for agricultural production in Australia, making the land highly sought after by early settlers for clearing and conversion to crops and pastures (Johnson 1964). As a consequence, the vegetation communities of this bioregion have undergone extensive changes since the end of World War II. During the course of agricultural development, particularly during the land development schemes of the 1960's and 70's, large tracts of native vegetation on arable soils throughout the bioregion were cleared. During this time, community attitudes towards native vegetation developed in the context of difficulties associated with its management and control, invariably leading to pervasive negative sentiments towards brigalow in many rural communities (Johnson 1964).

Only in recent years has land clearing in Queensland been more closely regulated as the benefits of retaining vegetation become more apparent. For example, the introduction of the Queensland *Vegetation Management Act 1999* protected a number of threatened and endangered vegetation communities. The recent ‘Brigalow declaration’ (2003), signed by 400 concerned scientists is further evidence of the important role played by native vegetation in maintaining biodiversity values and ecosystem function in Queensland landscapes. The declaration called for the control of clearing of mature native vegetation in Queensland, to prevent the local, regional and national extinctions that have been experienced elsewhere in Australia following extensive vegetation clearing – this declaration helped to convince the Queensland State Government to phase out broad-scale clearing by December 2006.

These policy changes should help to curb clearing rates in coming years. However, the consequences of years of rapid broad-scale habitat alteration throughout the Brigalow Belt bioregion, particularly in the years leading up to the introduction of tree clearing regulations (Figure 2.1), have had, and are likely to continue to cause, permanent detrimental effects on biodiversity and ecosystem function (Cogger *et al*. 2003; Carroll *et al*. 2004). Clearing of woody vegetation in Queensland, both legal and illegal, has continued at high levels in the Brigalow Belt bioregion since the introduction of the *Vegetation Management Act 1999*. For example, this bioregion has had the highest annual woody vegetation clearing rate in Queensland for 2003–2004, with 216,000 hectares cleared (Figure 2.1), comprising 45% of all state clearing for the 2003-2004 period. Approximately 96% of this land was cleared to make way for pasture for livestock (mostly cattle) grazing (Department of Natural Resources and Mines 2006).

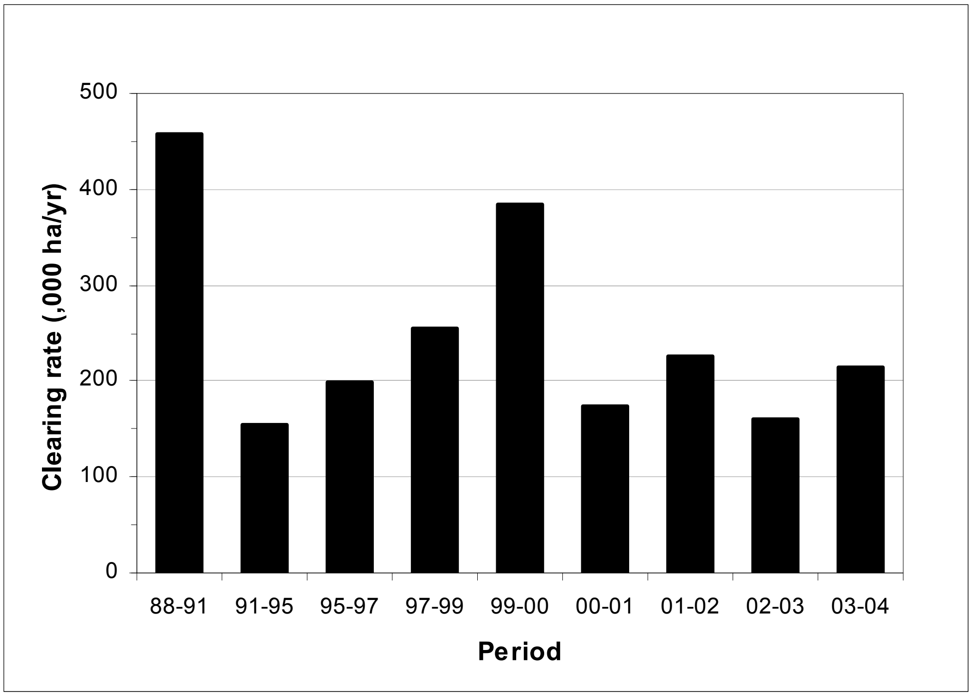

Figure 2.1. Average annual woody vegetation clearing rates in the Brigalow Belt bioregion for periods from 1988-2004 (Data source: Department of Natural Resources and Mines (2006)).

Compared with other temperate vegetation systems in Australia (e.g. eucalypt woodland (Saunders 1989; Bennett and Ford 1997) and buloke (Watson *et al.* 2000)), few ecological studies have been conducted in brigalow vegetation systems, particularly those of the Eastern Darling Downs (although see Johnson 1980; Dorricott *et al.* 1997; Fensham *et al.* 1998). Consequently, little is known about the impacts of clearing and habitat fragmentation on the distribution and abundance of plant and animal species in this region (Sattler and Webster 1984), or about the effects of landscape change on ecosystem function. Even less is known about the response of biodiversity in these areas to agricultural intensification and the status and trends of biodiversity and ecosystem function in the production matrix.

Despite the widespread land clearing, approximately 30% of the bioregion's native vegetation exists today as fragmented patches of varying size and condition, with less than 10% cover in some provinces of the bioregion (Department of Natural Resources and Mines 2006). However, only 2.2% of this remaining vegetation in the bioregion is protected in public reserves (Fensham *et* *al*. 1998), emphasising the importance of the contribution of vegetation fragments on private and leasehold lands to regional biodiversity conservation. The remaining native vegetation that exists outside public reserves is often subjected to degrading processes such as continued clearing or selective harvesting, grazing and weed infestation (Dorricott *et al*. 1998; Neldner *et al*. 2001). Hence, there is a clear need to better understand the range of ecological benefits provided by native vegetation on private land to prevent it from being undervalued and further degraded.

2.2 Site selection

A comprehensive spatial analysis of native vegetation communities of the southern Brigalow Belt bioregion was initially undertaken using GIS software, ArcView 3.2 (Environmental Systems Research Institute 1996), aerial photographs and spatial datasets provided by the Queensland Herbarium (Neldner *et al*. 2001). This analysis was used to identify and select potential study sites in various sub-regions of the southern Brigalow Belt bioregion.

Selection of sites was targeted at the regional ecosystem (RE) 11.9.5. This RE consists of shrubby open forest of *Acacia harpophylla* as a co-dominant with or without *Casuarina cristata* on Cainozoic to Proterozoic consolidated, fine-grained sediments in lowland areas on deep texture-contrast soils and cracking clays that are often gilgaied. *Geijera parviflora* and *Eremophila mitchellii* are predominant in the understorey, which can consist of semi-evergreen vine thicket species (Sattler and Williams 1999). This vegetation community was selected because it was once widespread throughout southern Queensland and was well represented on the available vegetation mapping at the time. The community is a nationally significant endangered ecological community (Sattler and Williams 1999).

Many of the sites initially selected on the basis of the spatial analyses and vegetation mapping datasets were found to be inappropriate for use in this study; this was chiefly a result of the broad nature of the vegetation classification system used by the Queensland herbarium (Neldner *et al*. 2001), in conjunction with the only available maps not being current enough to reflect changes in vegetation cover due to land clearing. For example, large areas of remnant brigalow/belah vegetation, surveyed and mapped before the introduction of native vegetation management laws in 1999 have since been completely or partially cleared (pers. obs.). Furthermore, upon site inspection, many of the patches identified as RE 11.9.5 on the maps were comprised predominantly of different vegetation types. Some difficulties in gaining access to private properties were also experienced due to negative landholder sentiment towards native vegetation management legislation in southern Queensland and suspicion of scientific research.

2.2.1 Study area description

Sampling sites were ultimately selected from a small area in the Eastern Darling Downs province of the southern Brigalow Belt bioregion in Queensland, Australia (Figure 2.2).

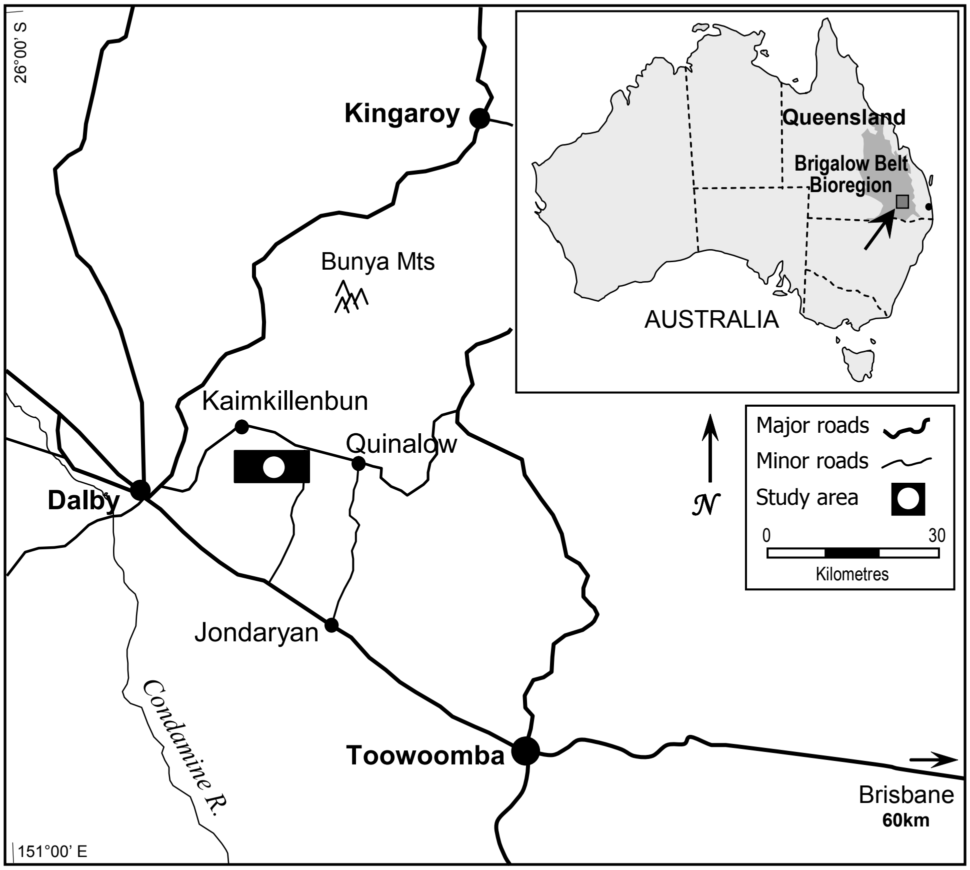

Figure 2.2. Map showing Queensland, Australia, the Brigalow Belt bioregion and the location of the study area in south eastern Queensland.

The nearest major town to the study area is Dalby (Lat -27^{o}18’ S, Long 151^{o}26’ E), which lies 340 metres above sea level. The climate of this area is classified as sub-tropical and it receives an average annual rainfall of 676 mm mostly during the summer months (Bureau of Meteorology, 2005).

Prior to European settlement, the deep, fertile and well structured cracking clays (vertisols) of the study area supported mixed associations of brigalow and belah vegetation (Harris *et al*. 1999). This vegetation association typically consists of a mix of brigalow (*Acacia harpophylla*)/belah (*Casuarina cristata*) as canopy species, *Geijera parviflora* (Wilga) and currant bush (*Carissa ovata*) in the understorey and a mixed assemblage of mainly perennial grasses (e.g. *Paspalidium caespitiosum* and *Chloris spp*) and semi-succulent forbs (e.g. *Einadia nutans, Enchylaena tomentosa*) in the groundlayer. Sedges such as *Cyperus gracilis* and the rock fern *Cheilanthes distans* are also common (Johnson 1964; Nix 1994). Today, mixed farming systems with summer and winter dryland cropping and limited grazing are the primary land uses (Harris *et al*. 1999).

2.2.2 Land use change in the study area 1945-2001

Preliminary examination of the study area using historical aerial photographs from 1945, 1971 and 2001 showed that unlike the recent extensive clearing in other parts of the Brigalow Belt bioregion (Wilson *et al*. 2000), the amount of original brigalow vegetation in the study area has remained virtually unchanged at about 6% since the early 1970s (Figure 2.3). Most of the original native woody vegetation in the study area was cleared by European settlers in the early 1940s, often followed by deep ripping, spraying and burning to overcome the problem of persistent brigalow ‘suckers’ (Johnson, 1964). Some of the cleared land was immediately used for cropping; however, large areas regenerated naturally to form semi-native grasslands, some of which remain today.

Detailed mapping and digitisation of historical aerial photographs showed that since the 1940s, much of this grassland has been gradually converted to intensively-managed cropping lands, such that only 25% of non-cropping land now remains in the landscape. This non-cropping land consists of small patches of remnant brigalow vegetation (5.8%) as well as uncultivated and previously cultivated (regenerating) native grasslands (19.5%) (Figure 2.3).

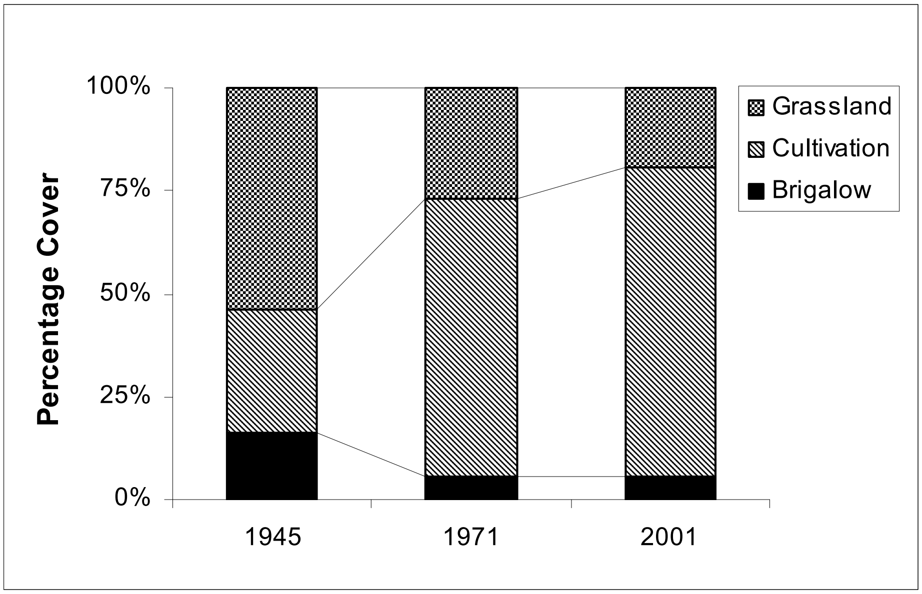

Figure 2.3. Proportion of Brigalow, Grassland (uncultivated and previously cultivated) and Cultivation from 1945-2001, derived using GIS and historical aerial imagery. Percentage cover was calculated using spatial data from within 2000m buffer areas around each brigalow patch (see section 2.4.3).

This study landscape is currently a typical agro-ecosystem, consisting of a mosaic of different land uses, largely dominated by cropping and grazing lands on the most productive soils. The remaining, uncultivated land consists of other vegetated landscape features such as remnant patches and linear strips in the form of windbreaks, watercourses and transport corridors. Remnant vegetation exists largely as patches smaller than 10ha.

Site selection was therefore limited by the availability of patches of brigalow/belah vegetation (henceforth referred to as Brigalow) on private land. Actual Brigalow sampling sites were selected on the basis of their condition and suitability for sampling following extensive ground-truthing. Sites were considered suitable if they were blocks (rather than narrow corridors) larger than 100 m x 100 m and if the structure and species composition of the dominant canopy and sub-canopy layers resembled pre-clearing (remnant) vegetation.

2.2.3 Description of Brigalow study sites

Twenty-two Brigalow patches were selected across the study area, ranging in size from 2 to 32 hectares (Figure 2.4). Selected Brigalow study sites were located on grey-brown cracking clays (pellic vertisols) on Walloon sandstone (LRA classifications 6a and 6b) (Harris *et al*. 1999).

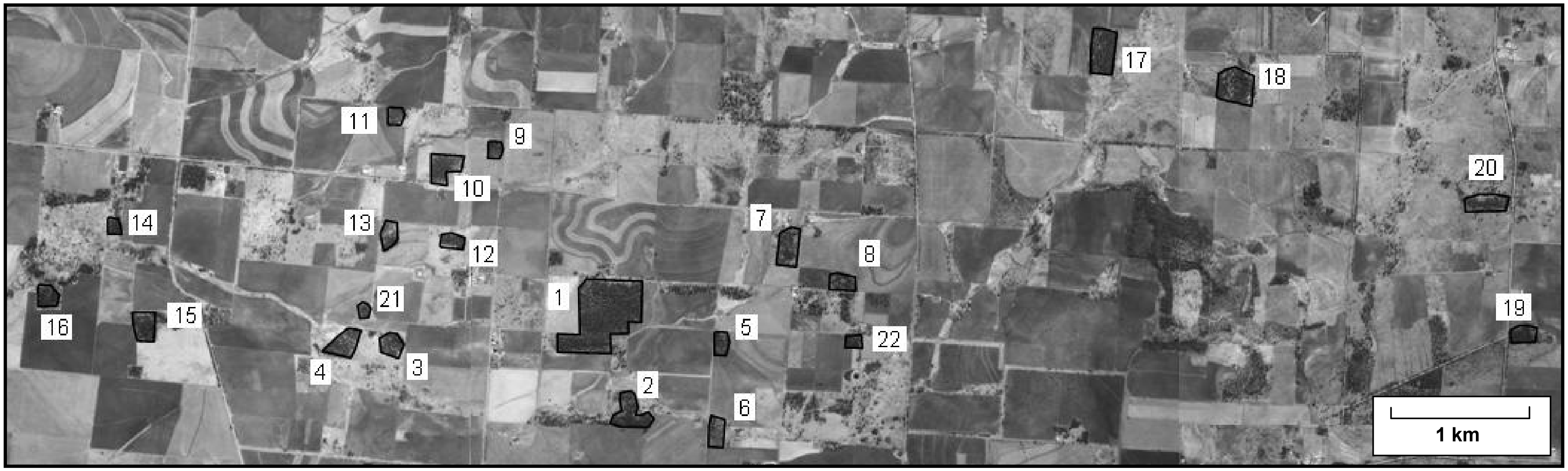

Figure 2.4. Aerial photograph of the study landscape taken in 2001, showing the 22 Brigalow patches used as the basis for study site selection

All Brigalow sites were disturbed from their natural (pre-European) state by grazing, weeds and/or other anthropogenic disturbances such as selective logging and vehicle tracks. Edges of the Brigalow vegetation were generally abrupt and adjacent matrix land uses comprised mostly cropping and small areas of semi-natural grassland (i.e. areas where brigalow has been cleared). Dryland cropping (cultivated) areas are mostly managed under minimum tillage and the most commonly grown species are sorghum in summer in rotation with millet, wheat and barley in winter (Harris *et al.* 1999). Characteristics for individual study sites are given in Table 2.1. Patch characteristics (e.g. area and shape) could not be calculated for individual matrix sites because these land uses were interconnected throughout the landscape and hence did not occur as discrete parcels of land.

Table 2.1. Brigalow study site characteristics, including patch area, land resource area (LRA), perimeter to area ratio, geographic location and adjacent land use in which matrix study sites were randomly placed. Grass_U = uncultivated grassland, Grass_P = previously cultivated grassland and Cult = cultivation

Site number	Area (ha)	LRA	Perimeter/ Area	Location		Adjacent land use
				Easting	Northing	
1	32.36	6a	115.10	351435	6998610	Cult
2	8.20	6a	54.95	351586	6997714	Cult
3	3.45	6a	44.38	349559	6998472	Grass_U
4	5.23	6a	51.68	349131	6998486	Cult
5	2.32	6a	36.71	352428	6998238	Cult
6	3.08	6a	39.51	352331	6997479	Cult
7	4.31	6a	39.04	353048	6999065	Cult
8	2.92	6a	40.83	353517	6998762	Cult
9	2.21	6a	37.19	350552	7000127	Grass_P
10	5.03	6a	46.81	350042	6999989	Grass_P
11	2.10	6a	33.65	349642	7000486	Grass_P/Cult*
12	2.12	6a	30.94	350124	6999341	Grass_U
13	3.03	6a	32.27	349531	6999424	Cult
14	2.39	6a	27.49	347145	6999631	Grass_P
15	5.13	6a	45.49	347421	6998707	Cult
16	2.22	6a	34.69	346511	6998983	Cult
17	8.33	6a	58.65	355931	7000527	Grass_U
18	8.13	6b	66.19	357103	7000183	Cult
19	3.70	6b	42.86	359462	6997741	Grass_P
20	5.08	6b	40.20	360303	6998528	Cult
21	1.51	6a	27.54	349338	6998762	Cult
22	1.33	6a	25.78	353586	6998210	Cult

*Site 11 changed from Grass_P to Cult after soil sampling and before plant and bird sampling. Locations are given as a grid references

2.3 Experimental design

2.3.1 Land management categories

The landscape was broadly divided into Brigalow and matrix habitat types. The matrix was further divided into three land use types according to past and current land management practices, giving the following four broad ‘land management categories’ (*sensu* Woodhouse *et al*. 2005) (Figure 2.5 a-d).

Brigalow

1) Remnant Brigalow vegetation that has never been cleared (‘Brigalow’, n = 22). Vegetation was often subjected to sporadic, low intensity grazing and occasional timber harvesting (Figure 2.5a)

Matrix

2) Grassland that has not been cultivated following clearing of the original Brigalow vegetation in the 1940s, with no deliberate addition of improved pasture species or fertiliser (‘Grass$_U$’ n = 3). Includes grassland subjected to frequent (8-12 months/ year) medium intensity cattle grazing and occasional spot spraying for woody weeds such as boxthorn (Figure 2.5b)

3) Grassland that has been previously cultivated but left fallow for 3-15 years (‘Grass$_P$’, n = 4). Includes regenerating grassland grazed frequently (8-12 months/ year), usually at medium intensity by cattle, and occasionally fertilised and sprayed with herbicide to control woody weeds (Figure 2.5c)

4) Recently (<2 yrs) cultivated land (‘Cultivation’, n = 12). The majority of cultivated sites were managed using zero or minimum tillage, with frequent (> twice/ year) herbicide application and annual fertiliser application. The most commonly grown crops were sorghum, millet and wheat with occasional, low intensity grazing of stubble (Figure 2.5d).

Figure 2.5a. ‘Brigalow’ land management category.

Figure 2.5b. ‘Uncultivated grassland’ (Grass_U) land management category in foreground and remnant Brigalow in background.

Figure 2.5c. ‘Previously cultivated grassland’ ($Grass_P$) land management category.

Figure 2.5d. ‘Cultivation’ land management category in foreground.

2.3.2 Sampling locations

At each study site, sampling points were located at the edge and core of the patch of the Brigalow vegetation, and at the edge and core of the adjacent matrix. These four sampling locations at each study site will henceforth be referred to as Brigalow core (BC), Brigalow edge (BE), Matrix edge (ME) and Matrix core (MC) (Figure 2.6).

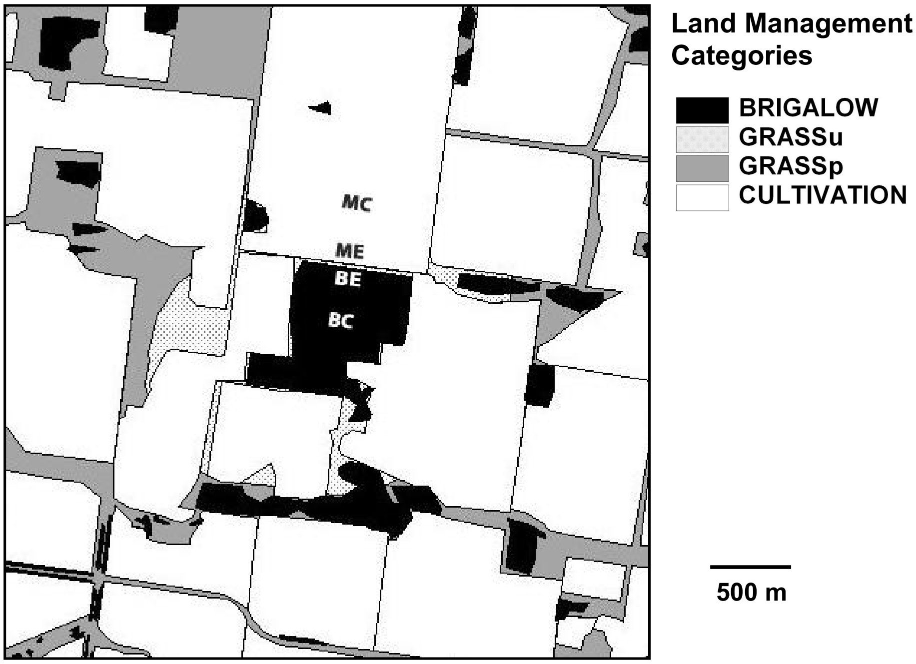

Figure 2.6. Schematic of a study site and the surrounding landscape from digitised aerial photographs, showing the four land management categories: 1) Brigalow; 2) uncultivated grassland (Grass$_{U}$); 3) previously cultivated grassland (Grass$_{P}$); and 4) Cultivation. Sampling points were located at Brigalow core (BC), Brigalow edge (BE), Matrix edge (ME) and Matrix core (MC).

Exact locations for each sampling point were selected using the following procedures. Co-ordinates for the centre of each study patch were determined using GIS Software ArcView version 3.2 (Environmental Systems Research Institute 1996). A GPS was used to locate the centre of each patch in the field. From the centre, a set of randomly generated numbers between 0 and 360 was used to select a compass bearing. A transect was established along this bearing between patch centre and patch edge and was extended along this bearing into the adjacent matrix. A different random number between 0 and 360 was selected if the line from the centre intersected adjacent vegetation patches, dams, cattle yards, houses or other highly disturbed areas.

Sampling points were established along the transect at the core and edge of the remnant vegetation and at the core and edge of the adjacent area of grassland or cropping. Brigalow remnant core (BC) was located at the centre of each of the 22 Brigalow patches. Brigalow remnant edge (BE), production matrix edge (ME) and production matrix core (MC) were positioned along a transect that extended from BC into the adjacent agricultural matrix (Figure 2.6). The distance between ME to MC was either equal to that between BC and BE, or a minimum of 100 metres.

Vegetation edge was defined as the limit of mature brigalow and/or belah trees in the patch of remnant vegetation. Sampling was conducted 5 metres in from the edge towards the BC sampling point. Matrix edge was defined as the limit of adjacent cultivation or grassland. This was usually clearly defined for cultivation but often quite diffuse for grassland sites. Sampling points at the matrix edge were positioned 5 metres from the edge into the matrix. To reduce the potential influence of the sampling points at Brigalow edge and matrix edge on each other, the matrix edge sampling point was offset from the transect line by 20 metres.

2.3.3 Ecological indicators of ecosystem function

Specific ecological indicators were selected to represent ecosystem function at a range of different trophic levels in brigalow agro-ecosystems (Table 2.2). Soil carbon was sampled at all 22 study sites, while plant and bird communities were sampled at those sites large enough to accommodate a 200 x 100 m belt transect (n=20, Table 2.2). Site 5 was inaccessible during the plant sampling period. Soil carbon and plant communities were measured at all four sampling locations (i.e. BC, BE, ME, MC). However, bird communities were measured only at BC and MC because of the small size of remnant Brigalow patches and the potential for overlap of sampling areas (Table 2.2).

Table 2.2. Number of study sites sampled, sampling locations and corresponding thesis chapter for each ecological indicator. Detailed descriptions of experimental procedures are provided in each chapter.

Indicator measured	No. of study sites	Sampling locations	Thesis chapter
Soil carbon (total, organic & labile)	**22**	BC, BE, ME, MC	3
Herbaceous plant communities	**19**	BC, BE, ME, MC	4
Bird Communities	**20**	BC, MC	5
Structural complexity	**20**	BC, MC	5

2.4 General analysis procedures

2.4.1 Univariate analyses

Differences in soil carbon fractions and plant richness, abundance and diversity data between land management categories were analysed using a two-way crossed analysis of variance (ANOVA) design. Bird data and habitat complexity data were analysed by one-way ANOVA using SPSS for windows (SPSS Inc. 2003). In all univariate analyses, residual plots were examined to see whether the assumption of equal variances was appropriate. To meet the assumptions of parametric tests, bounded data (percentages) were arcsine square root transformed (Winer 1971). After inspection of distributions, species richness data were log (x+1) transformed to address the distributional and variance assumptions required for linear models.

The study had an unequal number of treatments in each land management category. This type of 'unbalanced' design may have a number of statistical disadvantages. For example, different group means are estimated with different levels of precision, sometimes making interpretation difficult (Underwood 1997). If sample sizes are unequal, ANOVA F tests are less robust to violations of assumptions, particularly homogeneity of variances (Quinn and Keogh 2002). However, due to a limited number of available remnant Brigalow patches and significant variation in land management in the matrix, this type of design was unavoidable. Results will therefore be interpreted conservatively because of these statistical constraints, particularly when dealing with analyses that produce results that are close to the critical significance (*P*) level (Quinn and Keogh 2002).

2.4.2 Multivariate analyses

Plant and bird community abundance data were analysed using the multivariate approach developed by Clarke (1993) using PRIMER (Primer E-Ltd 2002). Non-metric Multi-Dimensional Scaling (nMDS), based on the Bray-Curtis similarity measure is used to give a visual 2 or 3-dimensional representation of the similarity of community assemblages at different sampling locations. Stress values are used to indicate the ability of nMDS to accurately portray the similarities between sites in a number of dimensions (Kruskal and Wish 1978; Jansen and Robertson 2001). Stress values < 0.1 are ideal; however, values <0.2 are regarded as a reliably accurate representation (Clarke and Warwick 1994), particularly if groupings are verified by other analyses. All nMDS ordinations were constructed with a minimum of 50 restarts. Analysis of similarity (ANOSIM) was used to determine statistical differences between groups (with up to 999 permutations). Where significant differences were found, the 'Similarity Percentage' (SIMPER) routine was used to determine which species contributed most to the similarity within and dissimilarity between groups (Clarke 1993; Clarke and Warwick 1994).

Regression analyses were performed using the stepwise multiple regression procedure in SPSS version 12.0.1 (SPSS Inc. 2003). In each regression the F-to-enter probability value was set at 0.05 and the F-to-remove value was set at 0.10. At each step in this procedure, the independent variable not in the equation which has the smallest probability of F is entered, if that probability is sufficiently small. Variables already in the regression equation are removed if their probability of F becomes sufficiently large. The method terminates when no more variables are eligible for inclusion or removal (SPSS Inc. 2003). This automated stepwise regression procedure is completely data driven and therefore has the potential to exaggerate the importance of the independent variables finally included. Hence, results from these analyses will be treated cautiously as a description of the data observed and to direct future studies.

2.4.3 Spatial data analyses

Aerial photographs (1:25000) of the study area from 2001, 1971 and 1945 were obtained from the Queensland Department of Natural Resources, Brisbane, Queensland. Images were scanned and registered using field-derived GPS co-ordinates and the SmartMap extension in ArcView version 3.2 (Environmental Systems Research Institute 1996). Using the GIS, concentric bands (buffer zones) at 500, 1000, 1500 and 2000 metre intervals were created around each Brigalow patch in each study site. Polygons of three land management categories (Brigalow, Grassland and Cultivation) within each buffer zone were manually mapped (digitised) by tracing the boundaries of areas of each land management category using the GIS. Grass_U and Grass_P were combined into a single grassland category in the spatial analyses because such subtle differences could not be detected using the available imagery. The proportion of the resulting three land management categories (i.e. Brigalow, Grassland and Cultivation) within each buffer area was calculated by summing the area of polygons for each land management category.

The concentric buffer zones around each Brigalow patch were used to distinguish between the effects of local-scale patch attributes and landscape context at different distances away from the study site. Because of the small size of the Brigalow patches and close proximity of the matrix sampling sites to the Brigalow patches, the data derived from these buffer zones was assumed to be appropriate for use in analyses of sample data from the matrix. The spatial analysis package ‘Fragstats’ (McGarigal and Marks 1995) was used to derive spatial metrics such as areal cover, number of patches (NumP) and mean patch size (MPS) of the three land management categories in each buffer zone. These data (Appendix 1) were used in Chapters 4 and 5 to explain the effects of landscape context on vegetation and bird communities.

CHAPTER 3

SOIL CARBON, AGRICULTURAL INTENSIFICATION & THE 'LANDSCAPE CARBON MANAGEMENT INDEX'

A significant part of this chapter has been published as:

Collard, S. & Zammit, C. (2006). Effects of land use intensification on soil carbon and ecosystem services in brigalow (*Acacia harpophylla*) landscapes of southeast Queensland, Australia. Agriculture, Ecosystems and Environment **117:**185-194.

3.1 Introduction

Soils provide a range of ecosystem services that play a crucial role in sustaining societies. These services directly benefit humans through the supply of goods such as food, fibre and pharmaceuticals and also contribute to the maintenance and regeneration of ecosystems (van der Putten *et al*. 2004). Soils play an important role in buffering and moderation of the hydrological cycle, providing physical support for plants, retention and delivery of nutrients to plants, disposal of wastes and dead organic matter, renewal of soil fertility and regulation of major element cycles (Daily *et al*. 1997). In agricultural landscapes, the organic components of soil, including soil biota, maintain biophysical processes such as aggregation and infiltration. These processes are essential for sustainable ecosystem function and agricultural production (Hendrix *et al*. 1990; Golchin *et al*. 1995; Bell *et al*. 1998).

The role of soil organic matter (SOM) in maintaining soil structure and productivity in agro-ecosystems is well recognised (Dalal *et al*. 1991; Carter 1996; Karlen *et al*. 1997). SOM has been widely used as an effective indicator of the functional response of soils to land use intensification (Carter 1996; Whitbread *et al*. 1998; Dalal *et al*. 2003). For example, declines of soil organic matter with increasing farming intensity and duration have been well documented in Australia (Dalal and Mayer 1986a; Gifford *et al*. 1992; Golchin *et al*. 1995) and elsewhere (Lucas *et al*. 1977; Mann 1986; Spaccini *et al*. 2001; Lemenih *et al*. 2005). SOM decline usually results from changes to soil structure caused by tillage, removal of biomass and increased mineralization and decomposition of exposed soils (Oldeman *et al*. 1990).

Soil organic carbon (SOC) has been used in the majority of recent monitoring programs to assess soil resource condition and trends (e.g. Cornforth 1999; Haynes 2000; Sparling *et al*. 2004; Karlen *et al*. 2001; Farquharson *et al*. 2003) and is regarded as a useful surrogate measure that integrates the influence of many different land management factors. However, short-term changes in SOC in response to altered land management are usually difficult to detect (Blair *et al*. 1995). Labile carbon fractions are increasingly being used in agro-ecosystems research because they respond more sensitively to changes in land management such as tillage (Dalal and Mayer 1986c; Biederbeck *et al*. 1994; Blair *et al*. 1995; Haynes 2000). Labile fractions of carbon are closely linked to soil microbial biomass, which accounts for only a small proportion of soil organic carbon (Powleson *et al*. 1987). Labile fractions can serve as indicators of the key chemical and physical properties of soils such as infiltration (Bell *et al*. 1998) and the availability of labile nutrients such as nitrogen, sulphur and phosphorus (Powlson *et al*. 1987).

To give a more complete representation of soil carbon dynamics, Blair *et al*. (1995) combined labile and non-labile carbon fractions to derive a carbon management index (CMI). Compared with a single measure such as organic carbon, Blair *et al*. (1995) proposed that CMI can be used as a more sensitive indicator of the rate of change of soil organic matter in response to land management changes, relative to a more stable reference soil. To date, the CMI has been used to monitor carbon pools only at farm or paddock scales (e.g. Blair *et al*. 1995; Whitbread *et al*. 2003). The CMI may also be potentially useful for measuring broader scale landscape function and soil ecosystem services.

In Australia, the conversion of extensive areas of native vegetation to pastoral and agricultural lands has led to widespread degradation of soil structure and fertility of arable landscapes (Dalal and Mayer 1986a; Commonwealth of Australia 2002). Under natural conditions, brigalow (*Acacia harpophylla*) vegetation is usually associated with deep, fertile and well structured cracking clays (vertisols) on lowlands (Sattler and Williams, 1999). Consequently the majority of brigalow lands have been converted to agricultural lands, with semi-natural grassland areas increasingly being converted to cropping. Such agricultural intensification often leads to local-scale changes in soil carbon levels (Dalal and Mayer 1986b) and may have broader implications for landscape functioning (Matson *et al*. 1997), carbon sequestration (Falloon *et al*. 2002) and climate change (Paustian *et al*. 2000).

In this chapter, total, organic and labile soil carbon concentrations in soil samples from the core and edge of patches of remnant brigalow vegetation are compared with those from the core and edge of adjacent managed grasslands and cultivated land (the production matrix). In particular, the study tests whether soils under remnant brigalow contain higher concentrations of carbon than those of uncultivated grasslands, previously cultivated (regenerating) grasslands and currently cultivated areas in the agricultural matrix. Total and labile carbon fractions were used to derive a carbon management index (CMI) as developed by Blair *et al*. (1995). A new 'landscape carbon management index' (CMI_L) is proposed as a tool for interpreting locally-derived carbon measurements across different spatial scales.

Hence, the main hypotheses examined in this chapter are:

1) There are differences in total, organic and labile soil carbon concentrations between land management categories of varying agricultural intensities

2) There are differences in total, organic and labile carbon concentrations between core and edge across land management categories

Furthermore, the research will explore the potential for locally-measured soil carbon measures to be aggregated to broader spatial scales.

3.2 Materials and methods

A brief outline of experimental treatments and method is given below. However, study site characteristics, experimental design and spatial analyses are described in more detail in Sections 2.2 – 2.4 of the general methods, Chapter 2.

3.2.1 Site and soil description

The field research was conducted in the Eastern Darling Downs province of the southern Brigalow Belt bioregion in Queensland, Australia. Nearby Dalby (Lat -27^{o}18’ S, Long 151^{o}26’ E), lies 340 metres above sea level (Figure 2.2).

Mixed farming systems with summer and winter cropping, interspersed with some grazing, are the predominant land uses in the area. Brigalow soils are typically pellic vertisols (FAO/Unesco 1974), characterised by high nitrogen content resulting from nitrogen fixation by root-nodulating bacteria (*Rhizobium* spp.) associated with brigalow root systems (Isbell 1962). Surface soil samples have pH 8-9 and are slowly permeable.

3.2.2 Study design

Twenty-two study sites were selected within brigalow (*Acacia harpophylla*) and Belah (*Casuarina cristata*) shrubby open forest (henceforth referred to as ‘Brigalow’) on cracking Cainozoic clay soils (defined by Sattler and Williams (1999) as ‘Regional Ecosystem’ 11.9.5). Sites were selected from the mosaic of available remnant patches in the landscape. The size of Brigalow patches sampled ranged from 2 to 33 hectares.

The study compares soil carbon from core and edge samples across the following four land management categories in a two-way crossed design:

1) Remnant brigalow that has never been cleared (Brigalow, n = 20);
2) Grassland that has been left uncultivated following clearing of the original brigalow vegetation (Grass_U, n = 3);
3) Grassland that has been previously cultivated but left fallow for 3-15 years (Grass_P, n = 4); and
4) Recently (<2 yrs) cultivated land (Cultivation, n = 13) (Figure 2.5).

3.2.3 Sampling and soil carbon analyses

Soil cores (10 cm diameter) were taken to 7.5 cm depth from five sampling points, no less than 2 metres apart within each treatment (i.e. BC, BE, ME and MC) at all 22 sites (n=88). This sampling depth was chosen to reflect the higher surface layer responsiveness of carbon to changes in land management (Janzen *et al*. 1992; Biederbeck *et al*. 1994). Surface litter was removed prior to soil coring and samples from each treatment were pooled and thoroughly mixed.

Pooled soil samples were sieved (<5 mm) to remove coarse debris (e.g. roots), air dried, mechanically ground to the appropriate particle size (refer to references in Table 3.1) and tested for total, organic and labile carbon concentrations using the methods described in Table 3.1.

Table 3.1. Summary of the methods used for measuring total, organic and labile carbon fractions

Carbon fraction	Method	Reference
Total Carbon	Weight loss-on Ignition	Storer (1984)
Organic Carbon	Wet combustion – Cr_20_7 oxidation + colorimetric analysis	Walkley and Black (1934), Sims and Haby (1971)
Labile Carbon	Oxidation 333mM $KMnO_4$ + spectral analysis (565 nm)	Blair *et al.* (1995)

3.2.4 Carbon Management Index

The Carbon Management Index (CMI) was calculated using mean values for total carbon and labile carbon from Brigalow core (BC) and Matrix core (MC) measurements across all sites using the procedure proposed by Blair *et al*. (1995):

1) Carbon Pool Index (CPI)

$$\textbf{CPI} = \text{total C}_{\text{Matrix}} / \text{total C}_{\text{Brigalow}}$$

2) Lability index (LI)

$$\textbf{LI} = \text{lability of C}_{\text{Matrix}} / \text{lability of C}_{\text{Brigalow}}$$

$$\text{where: lability of C} = \%\ \text{C}_{\text{Labile}} / \%\ \text{C}_{\text{Non-Labile}}$$

$$\text{and: C}_{\text{Non-Labile}} = \text{C}_{\text{Total}} - \text{C}_{\text{Labile}}$$

3) Carbon Management Index (CMI)

$$\textbf{CMI} = \text{CPI} \times \text{LI} \times 100$$

3.2.5 Landscape Carbon Management Index

A ‘Landscape CMI’ (CMI_L) was derived by multiplying the mean CMI value for each of three land management categories (Brigalow vegetation, Grassland (= $Grass_U$ and $Grass_P$ combined - it was not possible to separate the two grassland land management categories with available aerial and satellite imagery), and Cultivated land), by their proportion (%) in the landscape (L_P). The landscape comprised the 2000 m buffer areas around each study site. The resulting values for each land use were then summed to give the CMI_L:

$$\textbf{CMI}_{\textbf{L}} = \sum_n (\text{CMI} \times L_P)$$

3.2.6 Statistical analyses

Two-factor crossed analysis of variance (ANOVA) using SPSS version 12.0.1 (SPSS Inc., 2003) was used to compare mean concentrations of total, organic and labile carbon across core and edge samples and land management category (Sokal and Rohlf 1995). Percentage data for total and organic carbon fractions were arcsine square-root transformed prior to analysis to overcome the problem of bounded proportion data (Winer 1971). Residual plots and Levene's test (Levene 1960) indicated homogeneity of variance in all tested variables, suggesting the assumptions of the ANOVA were appropriate for the data. Significant differences within factors were tested using *a priori* contrasts between all possible combinations of treatments, with Bonferroni adjustments made to account for Type I error rates in multiple comparisons (Bonferroni 1936).

3.3 Results

3.3.1 Comparison of carbon concentrations

Mean total carbon concentration ranged from 2.0% at Grass$_P$ core to 6.1% Brigalow edge. Mean organic carbon ranged from 1.5% at Grass$_P$ core to 5.3% at Brigalow edge. Mean labile carbon content ranged from 3.2 mg/kg at Grass$_P$ core to 14.9 mg/kg at Brigalow edge (Table 3.2).

Table 3.2. Mean concentrations for total, organic and labile carbon (± *1 standard error*) at the edge and core of each land management category. Raw data are given in Appendix 2.

	Brigalow		**Grass$_U$**		**Grass$_P$**		**Cultivation**	
	Core	**Edge**	**Core**	**Edge**	**Core**	**Edge**	**Core**	**Edge**
Total (%)	5.92 (0.23)	6.14 (0.32)	4.23 (0.43)	4.63 (0.32)	1.98 (0.40)	2.08 (0.31)	2.03 (0.11)	2.37 (0.23)
Organic (%)	5.28 (0.22)	5.34 (0.26)	4.01 (0.31)	4.35 (0.20)	1.48 (0.38)	1.55 (0.24)	1.61 (0.12)	1.87 (0.21)
Labile (mg/kg)	14.45 (0.68)	14.87 (0.88)	9.72 (1.09)	10.17 (0.53)	3.15 (0.83)	3.44 (0.49)	3.37 (0.23)	4.10 (0.53)

There were significant differences between land management categories for total, organic and labile carbon concentration (ANOVA, $p<0.001$, Table 3.3), no significant differences between core and edge across all land management categories for total, organic and labile carbon ($p>0.05$), and no detectable interaction between main effects ($p>0.05$, Table 3.3).

Table 3.3. Two-way ANOVA results for total, organic and labile carbon concentrations. Values are F statistics with significance indicated

	Main effects		**Interaction**
	LMC	*Core vs Edge*	*LMC*Core vs Edge*
d.f.	3, 75	1, 75	3, 75
Total Carbon	108.0**	1.07^{ns}	0.11^{ns}
Organic Carbon	120.1**	0.76^{ns}	0.17^{ns}
Labile Carbon	135.8**	0.66^{ns}	0.11^{ns}

Concentration data arcsine-square root transformed, Values are F values **$p<0.001$, ns = not significant. LMC = Land management category

3.3.2 Comparison of soil carbon between land management categories

There were significant differences between land management categories for total carbon (Figure 3.1a, ANOVA $F_{3,87} = 110.8$, $p<0.001$), organic carbon (Figure 3.1b, ANOVA $F_{3,87} = 124.1$, $p<0.001$), labile carbon (Figure 3.1c, ANOVA $F_{3,87} = 140.3$, $p<0.001$). Mean total, organic and labile carbon levels were significantly higher in Brigalow than in any of the other land management categories (*a priori* contrasts $p<0.05$, Figures 3.1a, b, c). All three carbon fractions were significantly higher in uncultivated grassland ($Grass_U$) sites than previously (and currently) cultivated sites (*a priori* contrasts $p<0.05$, Figures 3.1a, b, c). There were no significant differences between currently (Cult) and previously cultivated ($Grass_P$) land management categories for any of the three measured carbon fractions (Figures 3.1a, b, c).

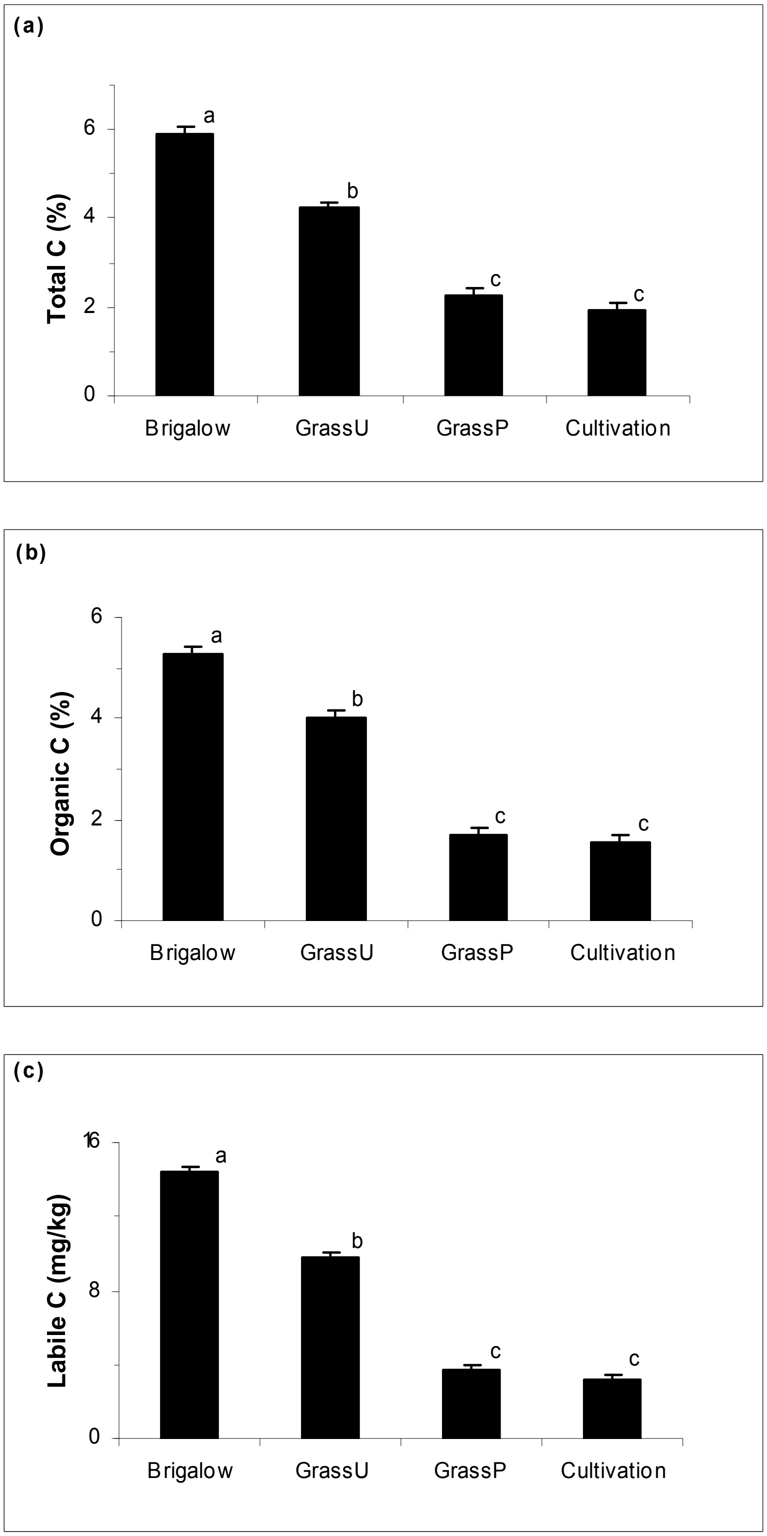

Figure 3.1. Mean values for (a) total, (b) organic and (c) labile carbon for different land management categories. Brig = Brigalow, Grass_U = uncultivated grassland Grass_P = previously cultivated grassland and Cult = currently cultivated; bars represent standard errors. Means sharing the same letter are not significantly different ($p>0.05$).

3.3.3 Residual levels of soil carbon and CMI, relative to Brigalow

The Carbon Management Index (CMI) was derived using percentage values for total and labile carbon, relative to the concentrations of these carbon fractions in the Brigalow reference sites. Mean values for residual carbon, relative to reference (Brigalow) soils for each matrix treatment are shown in Table 3.4. The overall proportion of soil carbon in the matrix land management categories, relative to that in Brigalow was highest for total carbon and lower for organic and labile fractions; an exception was organic carbon in the uncultivated grasslands (Table 3.4). A higher proportion of residual carbon was found in uncultivated grassland soils compared with previously and currently cultivated soils (Table 3.4).

Table 3.4. Summary of residual carbon for the matrix land management categories.

Matrix treatments	n	Residual carbon levels (%)		
		Total C	Organic C	Labile C
Grass$_U$	3	63.3 (*8.6*)	71.4 (*11.6*)	62.0 (*13.2*)
Grass$_P$	5	40.5 (*4.2*)	34.9 (*6.1*)	28.4 (*5.6*)
Cultivation	14	33.9 (*2.8*)	29.3 (*2.5*)	22.5 (*1.8*)

Residual levels are carbon values expressed as a percentage of soil carbon in reference soils under remnant vegetation (Brigalow). Values are means *(± standard error)* for total, organic and labile carbon from pooled matrix data. 'Grass$_U$' is uncultivated grassland, 'Grass$_P$' is previously cultivated (regenerating) grassland.

There were significant differences in the mean CMI between land management categories (Figure 3.2, ANOVA $F_{2,19} = 14.3$, $p<0.001$). The mean CMI was significantly higher in uncultivated grasslands than in both currently and previously cultivated areas (*a priori* contrasts, $p<0.05$) (Figure 3.2). There was no significant difference ($p>0.05$) between cultivated and previously cultivated land management categories (Figure 3.2).

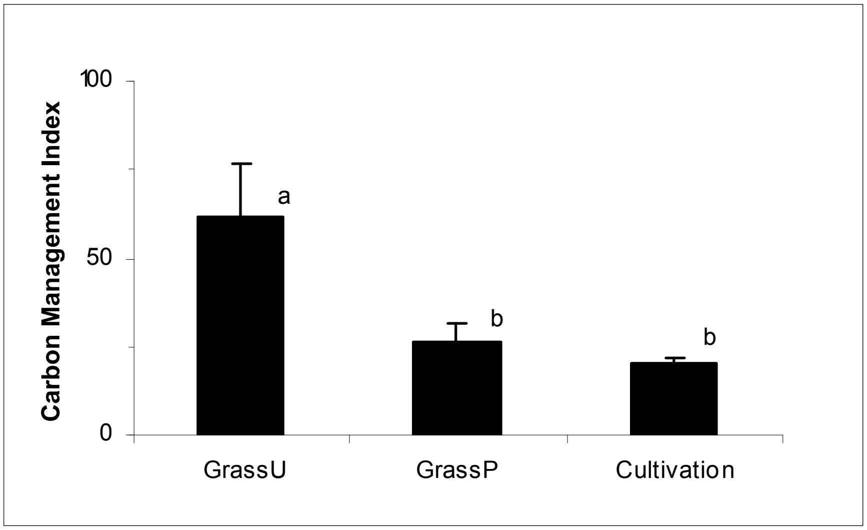

Figure 3.2. Mean values for the carbon management index for different land management categories, relative to soil carbon in Brigalow. $Grass_U$ = uncultivated grassland $Grass_P$ = previously cultivated grassland and Cult = currently cultivated; bars represent standard errors. Means sharing the same letter are not significantly different ($p>0.05$).

3.3.4 The landscape CMI – application across land management categories

The study landscape comprised 6.3% Brigalow vegetation, 74.7% cultivated land and 18.9% grassland (includes previously and currently cultivated), and the CMI_L for this landscape is 29.0 (Table 3.5).

Table 3.5. Proportion of the study landscape under each land use (L_P), the carbon management index (CMI) for each land use, the CMI_P (= L_P x CMI), and the landscape CMI (CMI_L) = $\sum CMI_P$.

Land Use	**L_P (%)**	**CMI**	**CMI_P**
Brigalow	6.3 (*0.3*)	100	6.3
Cultivation	74.7 (*0.6*)	20.4 (*1.7*)	15.2
Grassland	18.9 (*0.6*)	39.5 (*8.8*)	7.5
	CMI_L ($\sum_{CMIp}$) =		**29.0**

Values for L_P are means of percent cover (*± standard error*) within a 2000m radius of 22 study sites.

3.4 Discussion

3.4.1 Summary of main findings

The concentrations of the three measured soil carbon fractions decreased as land use intensification increased, with no detectable recovery of soil carbon in previously cultivated grasslands. There were no differences for any of the soil carbon fractions between core and edge in the same land management category. Homogeneity of soil carbon concentrations within discrete land management categories allowed for the aggregation of locally-derived measures of soil carbon to the landscape-scale using the $\mathrm{CMI_L}$.

3.4.2 Soil carbon decline in agro-ecosystems

The concentration and rate of decline of soil carbon vary considerably over time according to soil type, depth of measurement, rainfall, vegetation communities and management practices (Weil and Magdoff 2004). For example, Dalal *et al.* (2005) found lower organic carbon levels in surface soils (0-10 cm) under mulga (*Acacia aneura*) (0.69%) than under Brigalow (2.23%) soils. Dalal and Mayer (1986b) also recorded organic carbon levels of around 2% in Brigalow reference soils (0-10 cm) at nearby Chinchilla, Queensland compared with an average of over 5% for remnant Brigalow sites in my study (0-7.5 cm). This difference may be caused by variation in the depth of sampling, higher levels of plant organic matter and charcoal, or by past clearing or grazing management practices. However, despite these differences, the relative levels of soil carbon in this study are consistent with those observed in surface soils under long-term cultivation in other studies (e.g. Dalal and Mayer 1986b; Whitbread *et al.* 1998).

3.4.3 Response of SOM to land-use intensification

My research shows a marked decline in total, organic and labile carbon and CMI as land use shifts along the intensification gradient from remnant native vegetation (Brigalow) to cultivated land (Table 3.2). Other studies have shown similar declines in carbon in surface soils in cultivated areas compared with virgin soils, as a result of exposure from tillage and subsequent mineralization of organic compounds (Blair and Crocker 2000; Solomon *et al.* 2000; Murty *et al.* 2002). For example, Dalal *et al*. (2005) found that SOC had declined by 35% under wheat cropping 20 years after the original Mulga (*Acacia aneura*) vegetation had been cleared near St George, Queensland. Similarly, Solomon *et al*. (2000) found a 56% reduction of carbon in cultivated fields compared with native tropical woodland in Tanzania. This land-use intensification represents a significant loss of soil carbon and a corresponding reduction in soil condition across the landscape.

Contrary to my findings, some studies have detected higher carbon levels in uncultivated grasslands than in adjacent woody vegetation (e.g. Jenny 1941; Rasmussen and Collins 1991). Conant *et al*. (2001) noted that soil carbon content increased in 70% of studies examining the conversion of native land cover (mostly rainforest) to pasture. Significantly, net ecosystem carbon balance was found to decrease in 60% of these studies due to the removal of rainforest biomass (Murty *et al*. 2002).

In a review, Murty *et al*. (2002) also noted no significant overall change in SOC when land use changed from forest to pasture across a range of tropical and temperate systems. Changes in vertical distribution (rather than loss) of carbon in the soil profile in response to changing land use have also been proposed (Mendham *et al*. 2003; Lemenih *et al*. 2005). In Brigalow systems, lower soil carbon levels in uncultivated grasslands may be due to soil exposure and mineralization caused by disturbances associated with clearing original woody vegetation and ongoing management of persistent regrowth (Johnson 1964).

Other Australian studies have also shown greater declines of labile carbon compared with total carbon, indicating higher sensitivity of the labile fractions to farm management practices (Blair *et al*. 1995). For example, Blair and Crocker (2000) recorded average losses of 56% and 71% of total and labile carbon respectively, under a range of crop management practices in black soils (vertisols) near Tamworth, Australia after 20 years of cropping. Whitbread *et al*. (1998) recorded average losses of 37% total carbon and 54% labile carbon in grey clays (vertisols) after cropping durations ranging from 2 to 43 years (Table 3.6).

Table 3.6. Percentage decline of total and labile soil carbon, and the carbon management index (CMI) (± *standard error*), in various Australian surface soils (≤ 10 cm) under dryland cropping.

Study (year)	**Soil type**	**Cropping Duration (yrs)**	**Total C %**	**Labile C %**	**CMI**
Blair *et al.* (1995)	Red Earth *(Paleustalf)*	16-18	50.4 (*4.8*)	66.9 (*7.5*)	30.5 (*7.5*)
"	Brown Earth *(Palexeralf)*	4	30.2 (*0.0*)	50.9 (*0.0*)	45.0 (*0.0*)
"	Black Earth *(Pellustert)*	7	47.5 (*0.0*)	57.2 (*0.0*)	33.0 (*0.0*)
Whitbread *et al.* (1998)	Red Earth *(Alfisol)*	15-40	64.4 (*4.4*)	71.2 (*3.5*)	28.0 (*4.0*)
"	Grey Clay *(Vertisol)*	2-43	36.8 (*5.9*)	54.0 (*4.2*)	44.0 (*4.3*)
"	Black Earth *(Vertisol)*	25-40	37.3 (*2.2*)	33.6 (*8.6*)	66.5 (*9.5*)
Blair & Crocker (2000)	Black Earth *(Pellic Vertisol)*	>20	56.0 (*1.0*)	70.6 (*1.5*)	26.7 (*1.4*)
"	Red Clay *(Chromic Vertisol)*	>20	45.8 (*2.3*)	46.6 (*2.7*)	53.3 (*2.9*)
Whitbread *et al.* (2000)	Red Earth *(Ferric luvisol)*	>18	74.2 (1.2)	76.4 (2.9)	23.0 (3.4)
This study	Grey-brown clays *(Vertisols)*	>40	67.1 (2.8)	78.0 (1.9)	20.4 (1.7)

Values are means (± *standard errors*), expressed as a percentage of soil carbon in reference (uncultivated) sites, across land-use treatments in each study.

The levels of soil carbon at different locations in agro-ecosystems largely depend on soil type as well as the nature and duration of soil disturbances such as cultivation (Dalal and Mayer 1986b). The low residual carbon levels and CMI observed in the cultivated areas of the study landscape (Table 3.6) are likely to result from the long duration of continuous cultivation in these systems. These levels are also measured relative to soil carbon concentrations in remnant brigalow vegetation which, as noted earlier, were high compared with other studies in brigalow soils (Dalal and Mayer 1986b).

The combination of the different carbon fractions used in the CMI is considered a more informative indicator of overall change in carbon dynamics across the landscape than a single measure such as organic carbon. The CMI values for various Australian studies are compared in Table 3.6. To date, the majority of studies that have used the CMI have based their calculations on concentration values (e.g. Blair *et al*. 1995; Conteh *et al*. 1998; Whitbread *et al*. 1998; Blair and Crocker 2000; Whitbread *et al*. 2003). However, future studies should consider compensating for differences in soil bulk density, by expressing carbon content on an area, rather than concentration basis. Problems associated with volumetric analyses and quantifying bulk density in cracking clays soils (e.g. vertisols), can be overcome by determining bulk density at drained upper limit (Dalgliesh *et al*. 1998).

3.4.4 Application of the CMI at a landscape scale

Agricultural landscapes are traditionally managed at paddock or farm scales, with poorly understood links between production activities and landscape-scale ecosystem processes. Similarly, the CMI has been effectively used in the past to compare short-term changes to carbon dynamics in cultivated areas and grasslands at the paddock or farm scale (Blair *et al*. 1995; Conteh *et al*. 1998; Whitbread *et al*. 1998; Blair and Crocker 2000; Whitbread *et al*. 2003). This research extends the application of the CMI to the landscape scale, by extrapolating local soil measures to broader scales using GIS-derived land use classifications including woody vegetation, grasslands and cropping. The landscape carbon management index (CMI_L) can be used by land managers to combine the passive and active components of soil organic matter, and to enable decision-making across spatial scales.

The significant differences in soil carbon between remnant brigalow and the agricultural matrix were not apparent between core and edge in the same land use (Table 3.3). This observed relationship across land use boundaries suggests that there is little detectable net movement of organic matter across land use boundaries and that the relationship for soil carbon resembles a step function, rather than the hypothesised ecotonal relationships proposed by Reis and Sisk (2004) (Figure 1.2). Hence, in this landscape, different land uses (e.g. cultivated paddocks or patches of vegetation) can be considered discrete management units, in terms of soil carbon dynamics, based on their current soil carbon properties and management history. This defined boundary effect and observed homogeneity within land uses allows for extrapolation of local measurements to larger scales using GIS-based methods.

Other models have been used to link field-based soil measurements (including carbon) with spatially explicit databases such as geographic information systems (GIS) by aggregation, to produce broad-scale maps of soil resources and their response to changing land use patterns (e.g. Parton *et al*. 1987; Coleman and Jenkinson 1996; Paustian *et al*. 1997). In particular, Park and Cousins (1995) proposed a method for integrating GIS data with locally-derived soil health measures to provide management guidelines across scales. They identified the deficiencies of monitoring only the stable fractions of the soil organic matter pool and proposed the use of the more active biotic elements of soil. The CMI incorporates both the stable and responsive (biologically derived) fractions of the SOM pool, making it an ideal candidate for use in such models.

The CMI_L has the potential to be useful across landscapes of varying size and composition, and locally-derived measures of soil carbon can be accurately extrapolated in multi-use landscapes, provided that the types and duration of land management are well defined. In the landscape studied, only three broad land-use categories (brigalow vegetation, grassland and cultivation) were used to classify the landscape. Further division and spatial mapping of grassland and cropping types based on management regimes in the matrix (e.g. grazing, tillage practices, crop rotations) would provide additional information and allow stronger inference about the impact of land management on carbon pools across the landscape.

Spectral imaging could be used to differentiate more accurately between land uses (Wessman 1991).

3.4.5 Management options for enhancing soil carbon

Soil carbon levels showed a limited capacity to recover in previously cultivated areas following regeneration (< 15 yrs) by semi-natural grassland communities. A similar inability of soil carbon levels to recover after 14 years was found in successional old-fields in Virginia by Riedel and Epstein (2005). However, in contrast to these findings, other studies have shown that regenerating grasslands following cultivation have significantly enhanced soil carbon levels (e.g. Haynes 2000; San Jose *et al*. 2003). For example, Al-Kaisi *et al*. (2005) found that conversion from cropping to perennial grasslands raised SOC levels in surface soils (0-15 cm) by up to 52% over 10 years. Conant *et al*. (2001) also showed that changing from cropping land to grasslands in mostly temperate regions resulted in a mean annual increase in soil carbon content of >3%. San Jose *et al*. (2003) showed that savannah fallow enhanced SOC in old cropping lands by an average of 56% over 30 years. Total recovery of carbon to pre-agricultural levels after abandonment in a 'midcontinental' climate may take as long as 230 years (Knops and Tilman 2000).

Possible reasons for the slow recovery of carbon in this study include drier than normal conditions in the landscape during the sampling period (Bureau of Meteorology 2005), leading to low biological turnover (Six *et al*. 2002). Other factors include the relatively short duration of regeneration (less than 15 yrs), the small number of grassland sites sampled, and uncertain records of grazing intensity and management practices at the time of initial brigalow clearing.

Numerous studies have shown that SOM levels in agricultural lands can also be manipulated by changes to crop management such as crop rotation, tillage regimes, strategic fertiliser application and crop residue inputs (e.g. Grace *et al*. 1994; Haynes 2000; Gregorich *et al*. 2001; Magdoff and Weil 2004). Farquharson *et al*. (2003) modelled carbon dynamics in northern Australia and suggested that SOC could be improved by adding fertiliser, growing larger biomass crops and retaining stubble. Improvements in land management, such as crop rotations, have also been shown to increase labile fractions of soil carbon (Biederbeck *et al*. 1994; Bell *et al*. 1998; Whitbread *et al*. 2000).

3.4.6 Sustainable carbon management

Managing the chemical and structural properties of soils in agro-ecosystems is a vital component of sustainable production. In particular, soil processes such as nutrient cycling and carbon sequestration play an important role in regulating and maintaining beneficial ecosystem services (Daily *et al*. 1997). In this study, average soil organic carbon concentrations for cultivated land and previously cultivated grasslands were below the 2% considered to be the critical level of organic carbon required for maintenance of satisfactory soil aggregate stability (Greenland *et al*. 1975); productivity has been shown to decrease below this threshold (Janzen *et al*. 1992). However, the quantitative basis for such thresholds, particularly in different soils, is limited (Loveland and Webb 2003). Hence, in order to strengthen the applicability and interpretation of the CMI_L, research efforts should focus on refining threshold levels of total and labile carbon fractions from a range of soil types, below which soil functional capacity and the provision of ecosystem services diminish.

Soil carbon concentration varies considerably with depth, with higher concentrations generally recorded near the soil surface (Biederbeck *et al.* 1994). Various studies have also found that these surface soils are more responsive to changes in management. For example Dalal *et al*. (2005) found that organic carbon in the top 5cm was more responsive to change than at greater depths. Samples for the present study were taken only in the surface layer (0-7.5 cm), thereby maximising the likelihood of detecting response to changes in management. However, sampling to a greater depth would provide further information, particularly in relation to longer-term changes in soil carbon dynamics (Dalal and Mayer 1986b).

3.5 Conclusions

Soil carbon is widely used as an indicator of soil condition and may also reflect the duration and intensity of past agricultural management practices and hence represent an important component of ecosystem function. In this study, there were differences in total, organic and labile carbon concentrations between the different land management categories. All carbon fractions were significantly higher in remnant brigalow vegetation than in the adjacent agricultural matrix of cropping and grassland. In the matrix, uncultivated grasslands had significantly higher carbon levels than both currently cultivated areas and previously cultivated grasslands, with the latter showing no significant recovery of soil carbon after 3-15 years of natural grassland regeneration. Measurements of carbon concentration at the core and edge in the same land use were not significantly different, indicating that there was no detectable gradient of soil carbon across land use boundaries.

Consistent with other studies, active (labile) soil carbon components reacted more sensitively to changes in land management than total or organic carbon fractions. Hence, total and labile fractions were combined to derive the carbon management index (CMI), a more complete indicator of soil carbon dynamics. A new Landscape CMI (CMI_L) was developed, using a combination of locally-derived soil carbon measures and GIS–derived spatial data. The CMI_L is potentially useful as a spatially explicit tool for modelling the response of soil carbon and associated ecosystem services to changes in land management through time. In particular, it may be useful for monitoring changes in land use in response to agricultural intensification or ecosystem restoration.

CHAPTER 4

PLANT BIODIVERSITY AND AGRICULTURAL INTENSIFICATION

"The more diversified in habits and structures the descendants … become, the more places they will be enabled to occupy… If a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater dry weight of dry herbage can be raised in the latter than the former case" (Darwin 1872, as quoted in McNaughton (1993)).

4.1 Introduction

Modern agricultural ecosystems typically evolve along a gradient of increasing anthropogenic modification and structural simplification, from natural vegetation, through pastoralism, to an intensively managed mosaic of artificial monocultures (Matson *et al*. 1997; McIntyre and Hobbs 1999; Ryszkowski and Jankowiak 2002). Such agricultural intensification is often accompanied by a concomitant change (usually a decrease) in plant species composition and diversity (McLaughlin and Mineau 1995; Austrheim and Olsson 1999; McIntyre and Martin 2001; Fedoroff *et al*. 2005). This decrease may be caused by the combined effects of local-scale disturbances such as vegetation clearing and recurrent soil disturbance (Chalmers *et al*. 2005), and by broader-scale processes such as habitat fragmentation and consequent population isolation by simplification and homogenisation of the surrounding landscape (Fahrig 2003; Tscharntke *et al*. 2005). Plant assemblages that exist in an area may thus be influenced by both current and historical land use across a range of spatial and temporal scales (Koerner *et al*. 1997; Lunt and Spooner 2005).

Plant species diversity has been linked to ecosystem function and productivity (Naeem *et al*. 1994; Tilman 1997; Loreau *et al*. 2001; Hooper *et al*. 2005; Spehn *et al*. 2005) and to the stability and resilience of ecosystems (Tilman and Downing 1994; Wardle *et al*. 2000). Furthermore, there is increasing evidence to suggest that biodiversity, more generally, plays an integral role in sustaining ecosystem function and ecosystem services in production landscapes through self-regulation of processes such as nutrient cycling and pest control (Swift *et al*. 1996; Daily *et al*. 1997; Altieri 1999; Marshall *et al*. 2003). In particular, the number and relative abundance of plant and animal species with different functional characteristics are increasingly being recognised as important factors affecting the sustainable management of agro-ecosystems (Altieri 1999; Tilman *et al*. 2002).

The mix of these species is influenced by local-scale factors such as habitat and environmental quality (Duelli 1997), and by the composition and configuration of the surrounding landscape (Rosenzweig 1995; Wagner *et al*. 2000; Dauber *et al*. 2003). Efforts to conserve biodiversity and maintain ecosystem services in agro-ecosystems must therefore consider ecological communities and the processes affecting them, at a range of spatial scales (Baudry *et al*. 2000).

Local-scale disturbances such as soil tillage often lead to changes in soil structure and biological activity (McLaughlin and Mineau 1995; Chalmers *et al*. 2005) and to the continual reversion of plant and animal assemblages to early stages of biological succession (Altieri 1999; Austrheim and Olsson 1999). Succession in former agricultural lands and the mechanisms by which it occurs have been well documented in other countries (e.g. Connell and Slatyer 1977; Inouye *et al*. 1987; Pickett 1982; Pywell *et al*. 2002). However, comparatively few Australian studies have examined succession/regeneration following cultivation (exceptions are Arnold *et al*. 1999; Wong 2004), and in particular its effects on biodiversity and ecosystem function. This lack of research is probably due to the relative recency of agricultural land management in Australia, compared with European and north American systems.

Broad-scale fragmentation of native habitat and conversion to agriculture increases the area of remaining habitat that is exposed to edge effects (Saunders *et al*. 1991; Forman 1995). In agro-ecosystems, habitat edges are typically abrupt and may exhibit environmental gradients at different distances from the edge (Fox *et al*. 1997; Ross 2005). As patches of vegetation reduce in size, external disturbances are more likely to affect a greater proportion of the patch (i.e. as the perimeter: area ratio increases and core area diminishes with size and linearity (Forman 1995)). Hence, the plant species composition in small remnant patches, such as those sampled in this study (most smaller than 10 hectares), may be influenced by their proximity to the surrounding agricultural matrix (Usher 1987). They may be affected by microclimatic effects such as exposure to wind, higher levels of solar radiation (Matlack 1993), by competition from dispersive plant species from the surrounding matrix (Murcia 1995) or by fertiliser runoff and herbicide drift (Kleijn and Snoeijing 1997; Boutin and Jobin 1998).

Such edge effects may result in semi-natural plant associations, consisting of species that existed prior to fragmentation, combined with a new assemblage of disturbance-tolerant species from the surrounding landscape (Murcia 1995). This often leads to an increase in species richness in the area between two adjoining habitats (Angelstam 1992). Habitat edges that are adjacent to intensively farmed fields have been shown to have a higher prevalence of introduced and/or weedy plant species than edges adjacent to less intensively managed fields (Fox *et al.* 1997; Boutin and Jobin 1998). The edge influence may also vary according to the shape of the patch, the nature of the edge (Forman 1995) and the ability of the new plant species to colonise and compete with existing species (Murcia 1995). In small linear strips of habitat, this can have a significant impact on the overall integrity and species diversity of the patch.

In Australia, the broad-scale transformation of native vegetation to agriculture has been linked to local and regional declines in native biodiversity (Saunders *et al.* 1991; Bennett and Ford 1997). Other consequences include changes to ecological processes such as nutrient cycling (Prober *et al.* 2002a), hydrology (Hobbs 1993) and biological invasions across a range of spatial scales (Hobbs 1989; Hobbs and Huenneke 1992). The majority of ecological studies in Australian agricultural landscapes have been confined to fragmented or 'relictual' patches of relatively undisturbed, pre-European native vegetation, with the surrounding matrix of crops and secondary grassland considered a hostile environment for native species (e.g. Lambeck 1997; Fisher 2000). Comparatively few studies have examined the predominant matrix of cleared and disturbed cropping and semi-natural grazing lands. Those that have examined the matrix have focussed mainly on plant community responses to grazing in grasslands and grassy woodlands (e.g. McIntyre and Lavorel 1994; Tremont 1994; Lunt 1997; Fensham 1998; McIntyre and Martin 2001; McIntyre and Martin 2002). Even fewer studies have considered the more intensively managed cropping components of the matrix and their contribution to agricultural biodiversity (except see McIntyre and Martin 2001; Wong 2004; Chalmers *et al.* 2005; McIntyre *et al.* 2005).

Some areas of the Brigalow Belt bioregion have been subjected to almost continuous cropping for several decades and are now being left fallow because of decreasing soil fertility and increasing input costs to achieve profitable yields (Dalal and Mayer 1986). These ex-arable lands are typically colonised by dynamic communities of early successional plant species (Wilcox 1998). Studies of succession in former agricultural lands (old-field succession) in other countries have shown that vegetation communities readily move towards a semi-natural state (O'Connor 2005; Walker *et al*. 2004), thus restoring plant diversity and rejuvenating natural ecological processes such as nutrient cycling (Parker and Pickett 1997). Information about vegetation succession and the recovery of ecosystem processes following disturbance is important for our understanding of resilience and function (Hobbs and Norton 1996) and may assist with restoration and conservation of diversity and ecosystem services in agricultural landscapes.

In this chapter, I compare herbaceous plant communities (forbs and grasses) in four different land management categories along a gradient of agricultural intensification. Land management categories comprise continuous cropping and cultivation (Cultivation), previously cultivated areas allowed to regenerate (Grass$_P$), uncultivated grassland (Grass$_U$) and largely intact remnant brigalow vegetation (Brigalow). In addition, I compare plant communities sampled at the core and edge of patches of remnant Brigalow vegetation with those from the core and edge of adjacent managed grasslands and cultivation (the production matrix) to determine whether there are differences in plant communities both between and within land management categories. I also compare regenerating plant communities in areas that have been intensively managed in the past and discuss their potential for regeneration and recovery of biodiversity and the provision of ecosystem services.

Hence, the main hypotheses examined in this study are:

1) There are differences between herbaceous vegetation communities across land management categories of varying agricultural intensities

2) There are differences in herbaceous vegetation communities between core and edge across land management categories

3) Spatial configuration of the surrounding landscape (landscape context) affects herbaceous vegetation communities

4.2 Methods

4.2.1 Study sites

The remnant brigalow vegetation in the study area typically consists of a mix of *Acacia harpophylla* (brigalow) and *Casuarina cristata* (belah) as canopy species, *Geijera parviflora* (wilga) in the understorey and a mixed assemblage of mainly perennial grasses and forbs as groundcover (e.g. *Einadia nutans, Enchylaena tomentosa* and *Paspalidium criniforme*).

The study compares herbaceous vegetation communities (includes forbs and graminoids) from core and edge samples at 19 sites (Table 2.2) across the following four land management categories (resulting in 76 samples), in a two-way crossed design:

1) Remnant brigalow vegetation, never been cleared (Brigalow, n = 19);
2) Grassland that has been left uncultivated following clearing of the original brigalow vegetation (Grass_U, n = 3);
3) Grassland that has been previously cultivated but left fallow for 3-15 years (Grass_P, n = 4);
4) Recently (<2 yrs) cultivated land (Cultivation, n = 12).

Study site characteristics and experimental design are described in more detail in Section 2.3 of the general methods, Chapter 2.

4.2.2 Vegetation sampling

Vegetation sampling was conducted at the core and edge of each of the 19 Brigalow patches and at the core and edge of the adjacent grassland or cultivated area between 25th February 2003 and 7th April 2003. Belt transects (10 x 50m) were established at the core and edge of the Brigalow and the adjacent matrix at each study site. Ten (1 x 1m) quadrats were positioned at 5 metre intervals along the transect, at a randomly generated distance on either side of the centre line of the transect. Ground cover species (woody and herbaceous species <50cm in height) within the quadrats were identified to species where possible, and classified as native or non-native following the nomenclature of Stanley and Ross (1983) and Henderson (1997). In each quadrat, the percent projected foliage cover of each herbaceous plant species was estimated – this estimate included plants that were rooted outside the quadrat, but were projecting over the quadrat area. Estimates of the percentage cover of bare ground, leaf litter, graminoids and forbs were recorded.

Each species was assigned to a plant functional group, according to a combination of the following life history attributes. Classification decisions were made based on the literature (Stanley and Ross 1983; Henderson 1997) and field observations:

1) Herb type - monocots (grasses and sedges) or dicots (herbaceous forbs and woody dicotyledons <50cm);
2) Origin - exotic or native; and
3) Annual (including biennial) and perennial species.

4.2.3 Statistical analyses

Two-factor crossed analysis of variance (ANOVA) using SPSS version 12.0.1 (SPSS Inc., 2003) was used to compare means of total, native and exotic species richness (log transformed) and percentage cover (averaged across ten 1 x 1m quadrats and arc-sine root transformed) across core and edge samples and land management category (Sokal and Rohlf 1995). Residual plots and Levene's test (Levene 1960) indicated homogeneity of variance in all tested variables, suggesting the assumptions of the ANOVA were appropriate for the data. Differences within factors that were significant in the ANOVA were tested using *a priori* contrasts with Bonferroni adjustments made to account for Type I error rates in multiple comparisons (Bonferroni 1936). Data from the matrix core in site 9 (a Grass$_P$ site) were identified as outliers in residual plots (both before and after transformation) and were omitted from all analyses in this chapter. Non-parametric analyses (Chi-square tests) were performed on functional group data because these data did not meet the assumptions of parametric tests.

Patterns in community composition were investigated using PRIMER for windows version 5.2 (PRIMER-E Ltd, 2002). The frequency out of 10 quadrats and percentage cover of each plant species were used for these analyses. Similarity matrices were created using the Bray-Curtis similarity coefficient on square root transformed data. Non-metric multi-dimensional scaling ordinations (Kruskal and Wish 1978) and two-way crossed Analysis of Similarity (ANOSIM with 999 permutations; Clarke and Warwick 2001) were used to determine differences in plant community composition between core and edge and between land management categories. Similarity percentage analyses (SIMPER; Clarke and Warwick 2001) were used to determine the contribution of particular species to patterns of similarity within, and dissimilarity between, land management categories. Species that contributed up to 50% of the similarity or dissimilarity are presented here (after Hill *et al*. 2005; Eldridge and Freudenberger 2005).

Stepwise multiple regression (SPSS Version 12.0.1, SPSS Inc. (2003)) was used to determine the spatial variables that best predicted total, native and exotic species richness and percentage cover in both Brigalow and Matrix sites separately. Analyses were performed using GIS-derived measures of landscape composition and configuration, including patch area for each Brigalow site and cover of Brigalow, grassland (Grass_U and Grass_P combined) and cultivation at 500 - 2000m distances in the area surrounding the sampling site (refer Section 2.4.3 for methods). As many of the spatial measures were highly correlated in preliminary correlation analyses, the variables used in the stepwise regression were reduced to a more parsimonious set of spatial parameters prior to the analyses. The reduced set is shown in (Table 4.1). Correlations between the complete list of spatial variables (for species richness and cover) are presented in Appendix 3. Inferences from these analyses will only be made regarding broad variable types, rather than specific environmental variables listed in Table 4.1.

Table 4.1. Explanatory variables used in the stepwise regression models for plant communities, following removal of highly correlated variables. Structural biotic variables were different for the separate Brigalow and Matrix analyses, but the same spatial/ landscape context variables were included in both analyses.

Brigalow	Matrix
Structure (% cover)	**Structure (% cover)**
Trees 10-20m cover	Herbs & forbs cover
Shrubs >2m cover	Bare ground cover
Grasses cover	Litter cover
Herbs & forbs cover	
Logs cover	
Spatial / Landscape context	**Spatial/ Landscape context**
Patch Area	Patch Area
Grassland area 500m	Grassland area 500m
Number Grassland patches 500m	Number Grassland patches 500m
Brigalow area 2000m	Brigalow area 2000m
Grassland area 2000m	Grassland area 2000m
Number Brigalow patches 2000m	Number Brigalow patches 2000m

4.3 Results

4.3.1 General floristic patterns

A total of 148 herbaceous plant species was recorded in the study. Of these, 29 species were annual dicots, 14 species were annual monocots, 67 species were perennial dicots and 38 species were perennial monocots (Appendix 4). A total of 44 species (28 dicots and 16 monocots) were of exotic origin. One species listed as rare and threatened in the eastern Darling Downs province by Sattler and Williams (1999) was recorded during this study. The endangered perennial grass *Homophilis belsonii* was found in low abundance in 11 Brigalow sites with 3 records at Brigalow core and 10 records at Brigalow edge and a mean percentage cover across these sites of 1.1%.

Of all species recorded, 118 (79.7%) were found in Brigalow remnants, with 36 of these species (24.3%) unique to Brigalow sites (Table 4.2). Two species (*Bothriochloa decipiens* (native) and *Zinnia peruviana* (exotic)) were recorded in only uncultivated grassland (Grass$_U$) sites, with 8 species (7 native (including *Calotis lappulacea* and *Sporobolus creber*) and 1 exotic (*Digitaria eriantha*)) restricted to previously cultivated (Grass$_P$) sites. Fifty-one species were recorded growing in Cultivation sites, with 15 species (4 native (including *Chloris truncata* and *Vittadinia diffusa*) and 11 exotic (including *Anoda cristata*, *Schkuhria pinnata* and *Sorghum* sp.)) recorded only in this land management category (Table 4.2). Thirteen species (9 native (including *Atriplex semibaccata*, *Cynodon dactylon* and *Portulaca oleracea*) and 4 exotic (including *Salvia reflexa* and *Urochloa panicoides*)) were common to all four land management categories. Sixty-three species (43%) were recorded only in sites with no history of cultivation (i.e. in Brigalow or Grass$_U$ sites).

Table 4.2. Cumulative native, exotic and total herbaceous plant species richness recorded in each land management category. Values in parentheses are the number of plant species recorded exclusively in each category.

	Brigalow	**Grass$_U$**	**Grass$_P$**	**Cultivation**
	n = 38	n = 6	n = 7	n = 24
Native species	91 (36)	46 (1)	38 (7)	24 (4)
Exotic species	27 (7)	17 (1)	15 (1)	27 (11)
Total species	118 (43)	63 (2)	53 (8)	51 (15)

4.3.2 Species richness and cover

Mean native species richness ranged from 25 species per 10 square metres at Brigalow edge to 3 species in the same area at Cultivation core (Table 4.3). Mean exotic species richness ranged from 6 at Grass$_P$ core to 3 at Brigalow core. Mean total species richness ranged from 30 at Brigalow edge to 8 at Cultivation core. Native cover ranged from 64% at Grass$_P$ core to 6% at Cultivation core. Exotic cover ranged from 29% at Grass$_U$ core to 3% at Brigalow core. Total cover ranged from 75% at Grass$_P$ core to 19% at Cultivation core (Table 4.3).

Table 4.3. Mean native, exotic and total plant species richness (per 10 square metres) and percent cover (± *1 standard error*) at the edge and core of each land management category. Species richness (SR) and percent cover (Cover) values are means from 10 m^2**.**

		Brigalow		**Grass$_U$**		**Grass$_P$**		**Cultivation**	
		Edge	**Core**	**Edge**	**Core**	**Edge**	**Core**	**Edge**	**Core**
Native	**SR**	25.2 (1.2)	25.0 (1.1)	19.0 (1.7)	13.7 (1.3)	12.8 (2.1)	11.3 (1.9)	4.0 (1.0)	3.3 (1.1)
	Cover	37.1 (3.1)	31.4 (3.0)	48.0 (7.8)	46.3 (5.6)	60.4 (6.0)	63.7 (4.6)	10.5 (5.8)	6.0 (4.3)
Exotic	**SR**	4.3 (0.6)	2.7 (0.5)	4.3 (0.9)	4.3 (0.3)	5.8 (0.5)	6.0 (1.2)	4.9 (0.5)	4.6 (0.6)
	Cover	5.2 (1.7)	3.2 (1.3)	13.8 (5.4)	28.9 (13.2)	10.1 (3.5)	11.7 (4.3)	11.2 (3.7)	12.5 (4.8)
Total	**SR**	29.5 (1.1)	27.7 (1.2)	23.3 (2.6)	18.0 (1.5)	18.5 (1.9)	17.3 (1.2)	8.9 (1.2)	7.8 (1.5)
	Cover	42.2 (3.4)	34.6 (2.8)	61.8 (12.1)	75.1 (7.6)	70.5 (5.5)	75.4 (8.5)	21.7 (8.2)	18.5 (6.6)

There were no significant differences (ANOVA, P>0.05) between core and edge across all land management categories for total, native and exotic species richness and cover, and no interaction between main effects was detected (Table 4.4). Significant differences existed between land management categories for total, native and exotic species richness and percent cover (Table 4.4).

Table 4.4. Two way ANOVA results for vegetation attributes (total, native and exotic species richness and percent cover). Values are F statistics with significance indicated.

	Main effects		**Interaction**
	LMC	**Core vs Edge**	**LMC*Core vsEdge**
d.f.	3,75	1,75	3,75
Total SR	78.0**	1.6^{ns}	0.2^{ns}
Native SR	88.8**	1.1^{ns}	0.3^{ns}
Exotic SR	4.9*	0.6^{ns}	0.9^{ns}
TotalCover	21.1**	0.1^{ns}	0.6^{ns}
NativeCover	40.7**	0.3^{ns}	0.2^{ns}
ExoticCover	7.3**	0.6^{ns}	0.7^{ns}

Species richness data log (x+1) transformed, Cover data arcsine-square root transformed, *p<0.05, **p<0.001, ns = not significant. LMC = Land management category

Mean total and native species richness were significantly higher in Brigalow and significantly lower in cultivation than for any of the other land management categories (*a priori* contrasts p<0.05, Figure 4.1a & 4.1b). There were no differences in total, native or exotic species richness between Grass_U and Grass_P. Mean exotic species richness was significantly higher in Grass_P sites than in Brigalow but was not significantly different between other land management categories (Figure 4.1c).

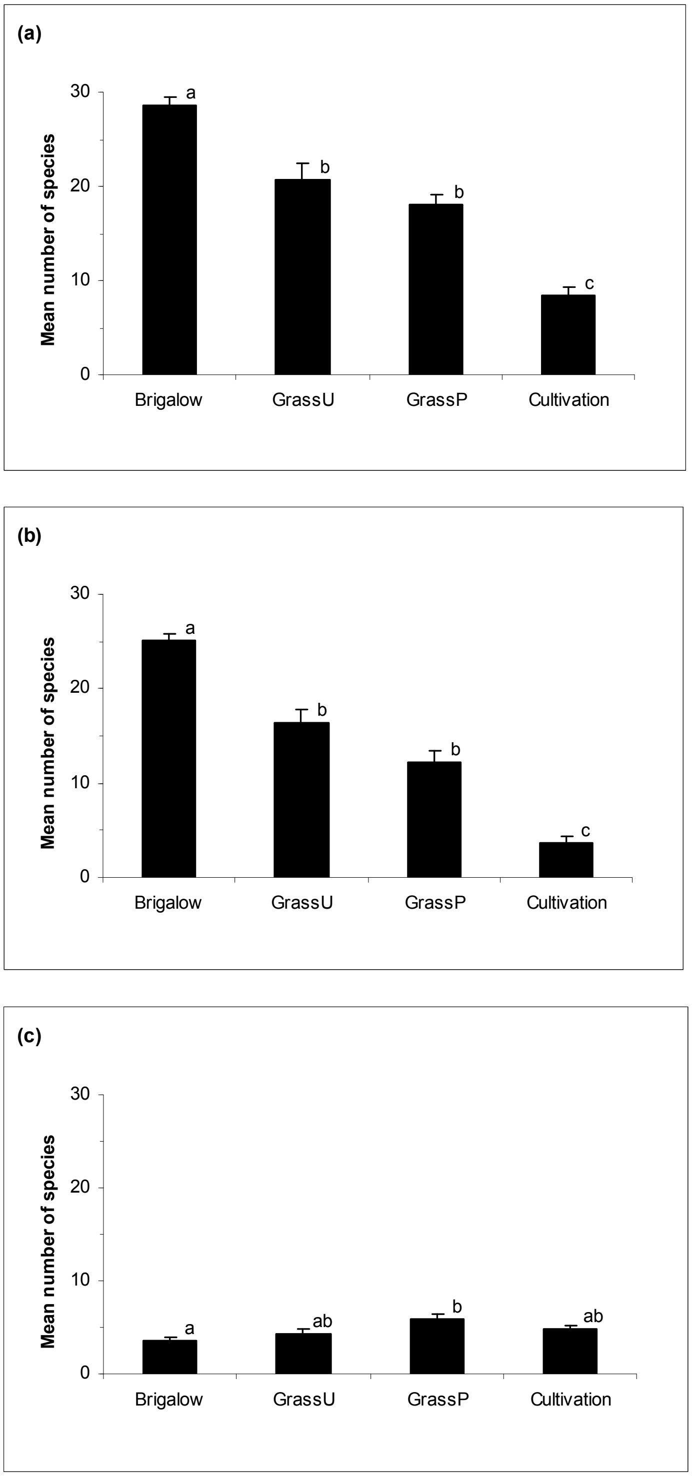

Figure 4.1. Mean plant species richness for (a) total, (b) native and (c) exotic species in Brigalow, uncultivated grassland (Grass_U), previously cultivated grassland (Grass_P) and current cultivation (Cultivation). Means sharing the same letter are not significantly different using untransformed data (*a priori* contrasts $p>0.05$). Error bars are standard errors.

Mean total and native cover were significantly lower in Cultivation than in any of the other land management categories, and significantly higher in $Grass_U$ and $Grass_P$ than in Brigalow or Cultivation (*a priori* contrasts $p<0.05$, Figure 4.2a & 4.2b). Exotic cover was significantly lower in Brigalow than in $Grass_U$ and Cultivation sites, but was not significantly different from exotic cover in $Grass_P$ sites. There were no significant differences in exotic cover between any of the matrix land management categories (Figure 4.2c).

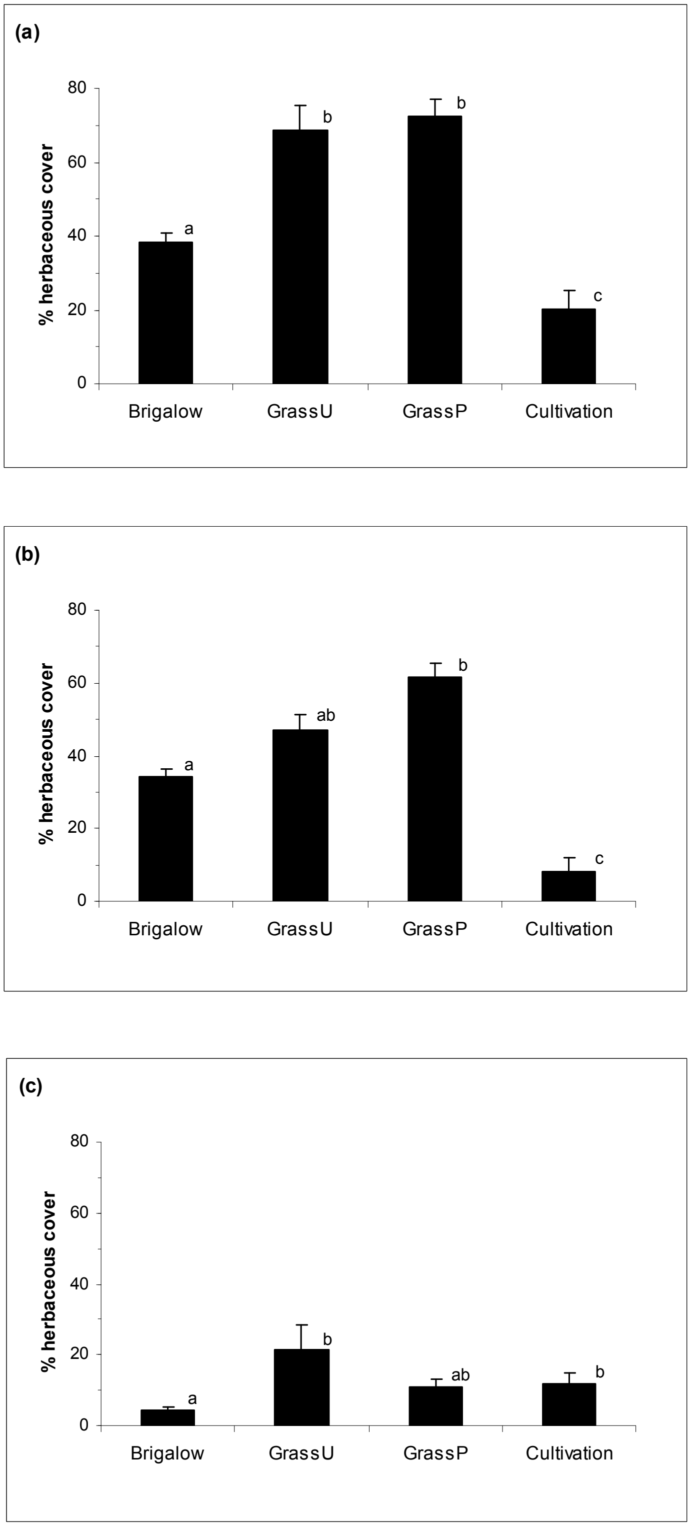

Figure 4.2. Mean percentage ground cover values for (a) total, (b) native and (c) exotic plant species in Brigalow, uncultivated grassland (Grass$_U$), previously cultivated grassland (Grass$_P$) and current cultivation (Cultivation). Means sharing the same letter are not significantly different using arcsine-root transformed data (*a priori* contrasts $p>0.05$). Error bars are standard errors.

4.3.3 Comparison of functional groups

There was a highly significant difference in distributions of richness ($\chi^2 = 414.11$, $p<0.001$) and percentage cover ($\chi^2 = 2245.48$, $p<0.001$) of vegetation across the four land management categories. Differences in species richness were due mainly to the higher than expected proportions in the richness of annual native monocots and dicots in cultivation, perennial exotic dicots in Grass_P and perennial native dicots in Brigalow. Species richness was lower than expected for perennial native species in cultivation and annual exotic species in Brigalow (Table 4.5). Differences in percentage cover were due mainly to lower than expected cover of annual exotic monocots in Brigalow, higher perennial native dicots in Brigalow, higher perennial native monocots in Grass_P, higher annual native monocots and annual exotic monocots in cultivation and lower than expected perennial native monocots in cultivation (Table 4.5).

Table 4.5. Mean (± *standard error*) plant species richness (SR) and percentage cover (Cover) of plants per 10m^2 in each land management category among functional groups. Functional groupings of species are shown in Appendix 5.

Functional Group		Brigalow	Grass_U	Grass_P	Cultivation
Annual native monocot (ANM)	**SR**	0.2 (0.1)	0.5 (0.3)	0.5 (0.3)	0.4 (0.1)
	Cover	0.1 (0.1)	0.3 (0.3)	0.3 (0.2)	4.6 (2.6)
Annual native dicot (AND)	**SR**	3.1 (0.2)	3.0 (0.7)	1.7 (0.6)	1.9 (0.3)
	Cover	2.5 (0.5)	1.7 (0.4)	0.5 (0.2)	2.1 (0.8)
Annual exotic monocot (AEM)	**SR**	0.4 (0.1)	1.2 (0.2)	1.0 (0.0)	1.9 (0.2)
	Cover	0.3 (0.1)	16.7 (7.8)	3.2 (2.1)	10.3 (2.8)
Annual exotic dicot (AED)	**SR**	1.5 (0.2)	1.7 (0.5)	1.7 (0.3)	1.8 (0.2)
	Cover	0.5 (0.2)	0.9 (0.5)	1.4 (0.4)	0.7 (0.1)
Perennial native monocot (PNM)	**SR**	7.5 (0.4)	6.5 (1.0)	3.8 (1.1)	0.8 (0.4)
	Cover	16.7 (1.6)	39.8 (4.2)	49.7 (10.8)	4.2 (2.8)
Perennial native dicot (PND)	**SR**	13.7 (0.6)	6.2 (0.8)	4.8 (1.1)	1.1 (0.3)
	Cover	14.9 (1.2)	5.4 (2.0)	4.6 (2.4)	1.0 (0.4)
Perennial exotic monocot (PEM)	**SR**	0.5 (0.1)	0.0 (0.0)	0.5 (0.3)	0.1 (0.1)
	Cover	3.0 (1.0)	0.0 (0.0)	5.7 (3.6)	0.5 (0.3)
Perennial exotic dicot (PED)	**SR**	1.0 (0.2)	1.5 (0.2)	1.8 (0.4)	0.6 (0.2)
	Cover	0.3 (0.2)	3.8 (3.3)	1.1 (0.4)	0.3 (0.1)

4.3.4 Community composition

An nMDS ordination of frequency data separated the four land management categories, with the distance between points reflecting the similarity of floristic composition (Clarke 1993). A gradient in floristic composition is evident on the ordination from Brigalow sites (on the right of the diagram) through grassland (Grass$_U$ and Grass$_P$) to cultivation (on the left) (Figure 4.3). Separate groupings of core and edge samples within the same land management category were not evident (Figure 4.3).

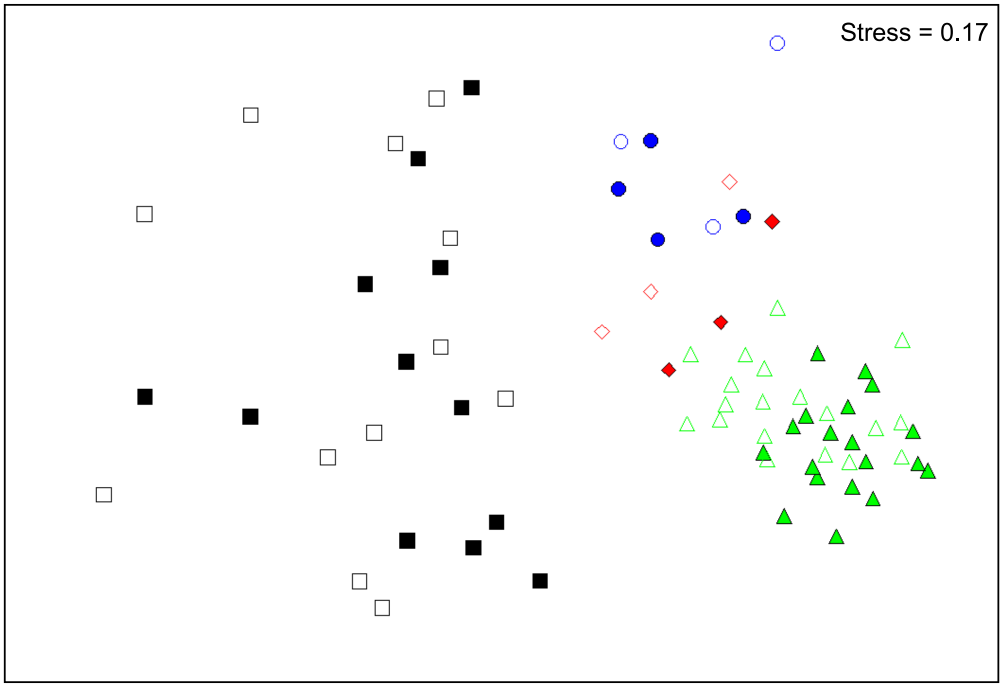

Figure 4.3. Two-dimensional ordination (nMDS) of plant frequency data showing core (shaded) and edge (open) within each land management category. ▲ = Brigalow core, △ = Brigalow edge, ◆ = Grass$_U$ core, ◇ = Grass$_U$ edge, ● = Grass$_P$ core, ○ = Grass$_P$ edge, ■ = Cultivation core, □ = Cultivation edge.

Two-way crossed Analysis of Similarity (ANOSIM) showed no significant differences in herbaceous plant community composition between core and edge across all land management categories (Global $R = 0.056$, $P = 0.046$). However, there were significant differences between land management categories (Global $R = 0.765$, $P = 0.001$). Pairwise tests showed significant differences ($P \leq 0.001$) between all land management categories except Grass$_U$ and Grass$_P$ (Table 4.6).

Table 4.6. Summary of Analysis of Similarity (ANOSIM) on plant frequency data. Values are R statistics (from pairwise tests) with significance level indicated (Global R = 0.776 Sign. level = 0.001)

	Brigalow	**$GRASS_U$**	**$GRASS_P$**
$GRASS_U$	0.741**	-	-
$GRASS_P$	0.940**	0.123^{ns}	-
CULT	0.877**	0.265*	0.398**

**p < 0.001, *p < 0.05, ns = not significant

Species that contributed up to 50% of the Bray-Curtis similarity within each land management category are listed in Table 4.7. The most abundant species in Brigalow included the annual native dicot *Tetragonia tetragonoides*, perennial native dicots such as *Einadia nutans* and *Sclerolaena tetracuspis* and perennial native grasses such as *Paspalidium criniforme* and *Cynodon dactylon*. Plant species with a mix of functional characteristics, including *Cynodon dactylon*, *Urochloa panicoides* and *Portulaca oleracea* contributed most to the similarity among $Grass_U$ sites. The native perennial grass *Dichanthium sericeum* and the exotic annual grass *Urochloa panicoides* contributed most to similarity in $Grass_P$ sites. Cultivation sites were characterised by a high abundance of annual exotic grasses such as *Sorghum* sp., *Urochloa panicoides* and *Echinochloa colona*, and by the annual native dicot *Portulaca oleracea* (Table 4.7). Similar general patterns were shown by an nMDS ordination and ANOSIM for percentage cover data (Appendix 6).

Table 4.7. Species contributing up to 50% of Bray-Curtis similarity, based on plant frequency data, for each land management category. Plant species are listed in decreasing order of their overall contribution to similarity (Cumulative %). Functional groups as indicated in Table 4.5.

LMC	**Species**	**Functional group**	**Average abundance**	**Cumulative %**
Brigalow	Average similarity = 40.03			
	Tetragonia tetragonoides	AND	5.47	11.26
	Einadia nutans	PND	4.74	22.01
	Paspalidium criniforme	PNM	4.71	30.19
	Sclerolaena tetracuspis	PND	3.71	37.00
	Enchylaena tomentosa	PND	3.05	43.32
	Cynodon dactylon	PNM	3.39	48.61
	Commelina cyanea	PND	2.53	53.61
Grass$_U$	Average similarity = 37.95			
	Cynodon dactylon	PNM	7.67	27.67
	Urochloa panicoides	AEM	5.83	46.35
	Portulaca oleracea	AND	3.50	55.11
Grass$_P$	Average similarity = 31.42			
	Dichanthium sericeum	PNM	8.29	37.45
	Urochloa panicoides	AEM	4.57	53.14
Cultivation	Average similarity = 17.01			
	Sorghum sp.	AEM	3.00	15.24
	Urochloa panicoides	AEM	2.58	30.22
	Echinochloa colona	AEM	2.63	44.40
	Portulaca oleracea	AND	2.88	56.46

Average abundance represents the average presence of species per plot within the land management category.

Land management categories that were significantly different according to ANOSIM (see Table 4.6) were tested using SIMPER. The average Bray-Curtis dissimilarities and the average abundance of species that contributed up to 20% of the dissimilarity between land management categories are listed in Table 4.8. Species contributing up to 50% (including data from Table 4.7) of the dissimilarity are shown in Appendix 7. In general, a combination of highly abundant species in one land management category and low abundance or absence of these species in the other land management category, contributed most to the differences between land management categories (Table 4.8, Appendix 7).

Seventeen species contributed up to 50% of the dissimilarity between Brigalow and Cultivation (Appendix 7): dissimilarity was influenced by the higher abundance of native species such as *Einadia nutans*, *Tetragonia tetragonoides* and *Paspalidium criniforme* in Brigalow (Table 4.8) and by exotic annual grasses such as *Sorghum* sp., *Urochloa panicoides* and *Echinochloa colona* in Cultivation (Appendix 7). Seventeen species contributed up to 50% of the dissimilarity between Brigalow and Grass$_U$ (Appendix 7): the high abundance of the grasses *Urochloa panacoides* and *Cynodon dactylon* in Grass$_U$ sites, and the high relative abundance of native species such as *Tetragonia tetragonioides*, *Paspalidium criniforme* and *Sclerolaena tetracuspis* in Brigalow, contributed most to the dissimilarity (Table 4.8). Thirteen species contributed up to 50% of the dissimilarity between Cultivation and Grass$_U$ (Appendix 7): dissimilarity was influenced most by the higher abundance of *Cynodon dactylon, Urochloa panicoides* and *Portulaca oleracea* in Grass$_U$ sites (Table 4.8) and by the annual exotic grasses *Sorghum* sp. and *Echinochloa colona* in cultivated sites (Appendix 7). Eighteen species contributed up to 50% of the dissimilarity between Brigalow and Grass$_P$ (Appendix 7): a large proportion of the dissimilarity could be attributed to the higher relative abundance of *Dichanthium sericeum* and *Urochloa panacoides* in Grass$_P$ sites, and by the high abundance of native species such as *Paspalidium criniforme* and *Tetragonia tetragonioides* in Brigalow (Table 4.8). Thirteen species contributed up to 50% of the dissimilarity between Cultivation and Grass$_P$ (Appendix 7): a higher abundance of the perennial native grasses *Dichanthium sericeum* and *Cynodon dactylon* and the annual exotic grass *Urochloa panacoides* in Grass$_P$ contributed most to the dissimilarity (Table 4.8). Five exotic species, including *Salvia reflexa*, *Panicum maximum* and *Verbena tenuisecta* were in higher abundance in Grass$_P$ sites than in Cultivation. The annual exotic grasses *Sorghum* sp. and *Echinochloa colona* were in higher abundance in Cultivation (Appendix 7).

Table 4.8. Average dissimilarity between land management categories (LMC) and the average abundance of plant species that contributed up to 20% of the dissimilarity between LMCs. Species are listed in decreasing order of their importance in discriminating the two sets of samples. Species contributing up to 50% of the dissimilarity are shown in Appendix 7.

Species	**Average abundance**		**Cumulative %**
Average dissimilarity = 94.22	**Brigalow**	**Cultivation**	
Einadia nutans	4.74	0	4.72
Tetragonia tetragonioides	5.47	0.96	9.42
Paspalidium criniforme	4.71	0	14.05
Sclerolaena tetracuspis	3.71	0	17.73
Cynodon dactylon	3.39	0.67	21.24
Average dissimilarity = 76.21	**Brigalow**	**Grass$_U$**	**Cumulative %**
Urochloa panicoides	0.87	5.83	5.11
Cynodon dactylon	3.39	7.67	9.98
Tetragonia tetragonioides	5.47	0.83	14.64
Paspalidium criniforme	4.71	0.33	18.99
Sclerolaena tetracuspis	3.71	1.33	22.24
Average dissimilarity = 87.69	**Cultivation**	**Grass$_U$**	**Cumulative%**
Cynodon dactylon	0.67	7.67	9.91
Urochloa panicoides	2.58	5.83	16.31
Portulaca oleracea	2.88	3.5	20.95
Average dissimilarity = 85.43	**Brigalow**	**Grass$_P$**	**Cumulative %**
Dichanthium sericeum	0	8.29	7.02
Paspalidium criniforme	4.71	0	10.94
Tetragonia tetragonioides	5.47	1.29	14.83
Urochloa panicoides	0.87	4.57	18.31
Cynodon dactylon	3.39	4.43	21.59
Average dissimilarity = 91.20	**Cultivation**	**Grass$_P$**	**Cumulative%**
Dichanthium sericeum	0.04	8.29	10.38
Cynodon dactylon	0.67	4.43	15.93
Urochloa panicoides	2.58	4.57	21.05

Average abundance represents the average presence of species per plot within each land management category. Cumulative % represents the cumulative influence of the species to the overall Bray-Curtis dissimilarity.

Dichanthium sericeum (Queensland Bluegrass) was mostly recorded in Grass$_P$ sites. The annual exotic grass *Urochloa panacoides* (Liverseed Grass) showed high abundance in uncultivated grassland (Grass$_U$) sites and had a large influence on dissimilarity in all Grass$_U$ comparisons. *Cynodon dactylon* (Couch grass) had a strong influence on dissimilarity in all comparisons and was found in high abundance in Brigalow, Grass$_U$ and Grass$_P$ sites (Table 4.8). These three grass species also contributed to a large amount of the dissimilarity in a SIMPER analysis of percentage cover data (Appendix 7).

4.3.5 The influence of landscape context

Stepwise multiple linear regressions revealed no significant predictor variables for total or exotic species richness in the Brigalow sites (Table 4.9). Mean grassland area at the 2000m scale explained 8% of the variation in species richness of native plants in Brigalow ($p<0.05$, Table 4.9). Overall, total, native and exotic species richness were not explained by the amount or spatial configuration of Brigalow in the landscape. However, the area of Brigalow in the landscape at the 2000m scale explained some of the variation in native cover in Brigalow sites. A significant amount of the variation in total, native and exotic cover was explained by remnant size and by grassland area at both 500 and 2000m scales (Table 4.9).

In the matrix sites, variation in total and native species richness and cover was significantly explained by grassland area at both 500 and 2000m scales. Remnant size also explained 13% of the variation in total cover. A significant amount of the variation in exotic cover in the matrix (37%) was explained by adjacent remnant size, the number of Brigalow patches at 2000m and the area of grassland at 2000m (Table 4.9). None of the measured structural biotic variables were significant predictors of plant species richness or cover in Brigalow or the matrix.

Table 4.9. Summary of stepwise regression results for the dependent variables total, native and exotic plant species richness and cover for: 1) Brigalow sites only and 2) Matrix sites only.

Characteristic	**Spatial Factors**	**d.f.**	**Adjusted R^2**	***B* (s.e.)**	***F***	***P*-value**
1) Brigalow sites						
TotalSR	No variables significant					
NativeSR	Grassland2000	1,37	0.08	-0.001 (0.00)	4.26	0.046
ExoticSR	No variables significant					
TotalCover	Grassland2000	1,37	0.15	0.002 (0.00)	7.63	0.009
	Grassland2000+Remnant Size	2,37	0.25	-0.182 (0.08)	7.21	0.002
NativeCover	Grassland500m	1,37	0.10	-0.003 (0.00)	4.95	0.032
	Grassland 500m + Brigalow 2000m	2,37	0.20	-0.002 (0.00)	5.72	0.007
ExoticCover	Remnant Size	1,37	0.11	-0.169 (0.07)	5.60	0.024
	Remnant Size+Grassland2000	2,37	0.22	0.001 (0.00)	6.25	0.005
2) Matrix sites (Grass$_U$, Grass$_P$ & Cultivation)						
TotalSR	Grassland500	1,36	0.13	0.007 (0.00)	6.44	0.016
	Grassland500+Grassland2000	2,36	0.21	0.002 (0.00)	5.68	0.007
NativeSR	Grassland500	1,36	0.21	0.014 (0.00)	10.79	0.002
	Grassland500 + Grassland2000	2,36	0.30	0.003 (0.00)	8.61	0.001
ExotiSR	No variables significant					
TotalCover	Grassland500	1,36	0.24	0.015 (0.00)	12.04	0.001
	Grassland500 + Grassland2000	2,36	0.30	0.004 (0.00)	8.74	0.001
	Grassland500 + Grassland2000 + Remnant Size	3,36	0.43	-0.522 (0.17)	10.22	0.001
NativeCover	Grassland500	1,36	0.30	0.017 (0.00)	15.03	0.000
	Grassland 500 + Grassland2000	2,36	0.40	0.003 (0.00)	11.43	0.000
ExoticCover	Remnant Size	1,36	0.22	-0.407 (0.09)	11.29	0.002
	Remnant Size + NumBrigP2000	2,36	0.30	0.006 (0.00)	8.69	0.001
	Remnant Size + NumBrigP2000 + Grassland2000	3,36	0.37	0.002 (0.00)	8.03	0.000

Species richness data log (x+1) transformed, Cover data arcsine-root transformed. Analyses were performed for each spatial variable, but only significant results ($p<0.05$) are displayed. R^2 values are cumulative for each variable tested.

4.4 Discussion

4.4.1 Responses of plant communities to agricultural intensification

This study shows differences in herbaceous plant species richness and composition between land management categories along a gradient of intensification from remnant brigalow, through grassland, to recent cultivation. Consistent with other studies, total and native plant species richness decreased with increasing intensity of agricultural management (Tilman 1997). In particular, cultivated areas that are subjected to continual disturbances such as tillage and herbicide application, had significantly lower total and native richness than any of the other land management categories. Similarly, Chalmers *et al*. (2005) found that total plant species richness was lower under high levels of soil disturbance than moderate and low levels, and that the abundance of most native perennial species decreased with high soil disturbance.

Other studies show that soil disturbance has immediate negative effects on native species richness and cover, and leads to decreases in native perennial species and increases in the richness and cover of exotic annuals (Fensham 1998; McIntyre and Lavorel 1994; Wong 2004). In particular, Fensham (1998) noted a transition from native to exotic colonisation (e.g. *Chloris virgata* and *Eragrostis cilianensis*) with increasing mechanical disturbance on the Darling Downs. McIntyre and Martin (2001) showed that sown pastures and crops in Australia's sub-tropics contained 30–50% of the native species found in less disturbed land uses such as native (unfertilised) pasture and remnant vegetation. In my study, recently cultivated and cropped areas were characterised by a high abundance of annual exotic monocots such as *Echinochloa colona* and *Urochloa panicoides*. These cultivated areas had the lowest native species richness of all land management categories, with less than 16% of the native species richness recorded in adjacent brigalow remnants. Similar to the findings of O'Connor (2005), cultivated areas made only a small relative contribution to the overall native plant diversity in the studied landscape. Species richness of exotics in sites did not vary significantly across three of the four land management categories, a finding supported by McIntyre and Martin (2001).

Remnant brigalow vegetation systems contained higher herbaceous plant species richness than areas of cleared/uncultivated grassland (Grass_U) areas. This is contrary to some other Australian studies in grassy eucalypt woodlands in the tropics and sub-tropics in Queensland, which have shown that tree removal without cultivation, may actually enhance (McIvor 1998), or not affect species richness (Fairfax & Fensham 2000; McIntyre and Martin 2001). However, the lower species richness in my grassland sites could be attributed to soil disturbances associated with historical tree clearing practices such as deep ripping and burning to suppress persistent brigalow regrowth (Johnson 1964). This may have caused the reversion of plant communities to early stages of succession following clearing, allowing competitive exotic species to colonise and potentially affecting shade-tolerant species of the original brigalow systems (Scanlan 1991).

According to information provided by landholders, grazing was generally infrequent and at low intensity across all land management categories, with grassland areas potentially subjected to more intensive grazing pressure at certain times, relative to adjacent brigalow and cropping areas due to higher palatable grass cover. This grazing may have affected the grassland plant communities, although Fensham (1998) showed that native grassland plant communities on the Darling Downs can tolerate, and may even require, moderate levels of grazing, with only a few species showing a high sensitivity to grazing disturbance.

4.4.2 Edge effects

Despite the small size of the sampled brigalow patches and hence, the potential for high edge to area ratios (see Table 2.1) and consequent edge effects (Forman 1995), there were no detectable differences between core and edge for plant species richness and cover in any of the land management categories, including brigalow remnants. Furthermore, contrary to the results of Fox *et al*. (1997) and Beer and Fox (2000), who sampled in small rainforest remnants, I found no significant difference in overall herbaceous species richness and composition between remnant core and edge. These findings suggest that the vegetation communities in these small brigalow remnants were homogeneous throughout. Due to limited information on the original plant assemblages in Brigalow in the study area, it is not clear whether this homogeneity implies that the patches consist only of edge-preferring plant species, or whether the plant assemblage is semi-natural, comprising species from the original community, mixed with ubiquitous edge-preferring species. However, given the high species richness in Brigalow compared with other land management categories in the surrounding landscape matrix, it is likely the latter is true; to verify this finding, comparisons are needed with undisturbed, contiguous brigalow/belah forest. Since no such 'reference' forest exists in the immediate vicinity of the study landscape, no strong inferences can be made about community composition and edge preferences of different plant species. Furthermore, the disturbed remnant brigalow patches sampled are typical of the remaining forest remnants on private land throughout the southern Brigalow Belt bioregion.

Many ecological studies have shown patterns of increased species richness at habitat edges (Angelstam 1992; Risser 1995). These 'ecotones' often contain higher species diversity than either of the two adjacent habitats because of the composite nature of the species assemblage (Murcia 1995). However, unlike the elevated plant species richness at remnant rainforest edges found by Fox *et al.* (1997), the sampled brigalow remnants had similar species richness throughout. The comparatively open brigalow vegetation may be more susceptible to high levels of disturbance by grazing, spray drift, exotic species or increased light intensity, leading to the observed homogeneity in plant species richness throughout the patches. The alternative hypothesis, that these patches are resilient to edge effects is unlikely, given the recorded presence of exotic species at the core of these patches, suggesting some degree of disturbance throughout.

Invasion of native communities by exotic species is widely recognised as a key threatening process to species diversity (Hobbs 1989; Lodge 1993; Adair and Groves 1998). For example, exotic species (e.g. buffel grass, woody weeds) can change both structure and function (Lambert and Graham 1996; Fairfax and Fensham 2000). Exotic invasion is often closely associated with some form of disturbance (often anthropogenic) such as vegetation clearing, livestock grazing or nutrient enrichment (D'Antonio *et al.* 1999; Leishman 2005). This was apparent in the studied sites, as evidenced by higher mean richness and cover of exotic species in grassland sites than in brigalow. However, other studies in the Darling Downs have noted that threats to native grassy communities caused by exotic species competition may not be as severe as in temperate systems elsewhere in Australia (Fensham 1998; McIntyre and Martin 2001).

4.4.3 Regeneration of former agricultural lands

Results from Grass$_P$ samples provide strong evidence of regeneration of herbaceous semi-natural plant communities following cultivation. After only 3-15 years since last cultivated, these communities showed no detectable differences in species richness or community composition when compared with uncultivated grasslands. This rapid regeneration by plants in previously cultivated systems contrasts with the lack of recovery shown by soil carbon and may represent the first steps in the recovery in ecological function and resilience in these systems. Differences in the recovery of these two indicators in previously cultivated grasslands will be described in more detail in Chapter 6.

Restoration of former production lands through natural or facilitated regeneration is an increasingly common method used in agricultural landscapes to enhance native biodiversity and ecosystem function, both in Australia (Lunt 1997; Arnold *et al*. 1999; Prober 2002*b*) and overseas (Korthals *et al*. 2001; Kardol *et al*. 2005). Extended fallow periods in retired cropping lands usually result in the regeneration of species rich semi-natural grassland plant communities (Walker *et al*. 2004; O'Connor 2005). Establishment of native species in such ex-arable lands may be influenced by various factors such as 'botanical legacy' (Kardol *et al*. 2005), propagule availability (Bakker and Berendse 1999; Pywell *et al*. 2002), assembly rules (Hansson and Fogelfors 1998; White and Jentsch 2004), environmental stochasticity, or other factors caused by management history at the site such as fertiliser application and grazing intensity (Critchley *et al*. 2002; Dorrough *et al*. 2004; Wong 2004). Restoring different components of the plant assemblage may also require different lengths of time (Parker and Pickett 1997). Studies have shown that initial regeneration is dominated by species in the soil seed bank (Lunt 1997; McIntyre and Martin 2001). As plants from surrounding areas colonise, species diversity has been shown to increase commensurate with time since ploughing (Austrheim and Olsson 1999).

In agricultural landscapes elsewhere, land abandonment in response to food surpluses and diminishing biodiversity, has provided researchers with many opportunities to study plant succession (e.g. Parker and Pickett 1997). In Australia, decreasing soil fertility and yields, commodity prices and uncertain climatic conditions are drivers for land abandonment and agricultural 'de-intensification' (Diamond 2005). However, such abandonment of ex-arable lands provides opportunities for the regeneration of semi-natural ('novel') plant communities (Fensham 1998; Hobbs *et al*. 2006). Natural regeneration in these ex-arable areas, even if only for short periods, is likely to have positive implications for biodiversity and may help to enhance ecosystem function and resilience.

Annual plants species are typically the first to colonise disturbed areas and tend to be dominated or replaced by perennial species (Corbet 1995; Wilcox 1998). For example, Fensham (1998) noted that areas of disturbed soil in the eastern Darling Downs are susceptible to colonisation by exotic species such as *Eragrostis cilianensis*. He also found that the most widespread exotic species across four native vegetation types (red gum woodland, grassland, poplar box woodland, hill woodland) were *Conyza bonariensis*, *Urochloa panicoides*, *Opuntia tomentosa*, *Rapistrum rugosum*, *Verbena officinalis*, *Verbena tenuisecta*, *Cyperus rotundus* and *Opuntia stricta*. Six of these species were common across multiple land management categories in the landscape. In my study, the most common early colonising species in areas that were under current cultivation were annual exotic monocots such as *Urochloa panicoides* and *Echinochloa colona*.

In the previously cultivated ($\mathrm{Grass_P}$) communities (> 2 years since cultivation), the dominant exotic annual colonisers (e.g. *Urochloa panicoides, Echinochloa colona*) had been largely replaced by the native perennial grass *Dichanthium sericeum* (Queensland bluegrass) and by a range of other native perennials. Comparisons of species richness, percentage cover and community composition showed that there were no differences between previously cultivated ($\mathrm{Grass_P}$) and uncultivated (Grass$_U$) grasslands. However, the SIMPER analyses suggest that the abundance of certain grassland species were different between the two groups. In particular, *Dicanthium sericeum* was found in much higher abundance in the more disturbed Grass$_P$ sites. In its natural state, this species grows in diverse grassland associations that are considered to be endangered ecological communities in Queensland (Sattler and Williams 1999; Commonwealth of Australia 2001). Interestingly, this grass species was not found in any of the sampled brigalow patches, suggesting perhaps that it is a shade-intolerant Andropogoneae (Scanlan and Burrows 1990), and that it may have colonised these areas in response to the clearing of the original brigalow vegetation. Fensham (1998) also reported that disturbed ground on basalt and alluvial soils in the Darling Downs is commonly colonised by this native grassland species. This species is seen by graziers as a beneficial grass species, valuable for production (Roberts and Silcock 1993). The successful regeneration of Queensland bluegrass in low fertility, ex-arable farmlands may provide farmers with a viable alternative to intensive cropping practices.

Other studies have also shown that native perennial grasses colonise rapidly following cultivation (Robinson *et al*. 1993; Garden *et al*. 2001). For example, in highland Sourveld grasslands of South Africa, abandoned cropland reverted to near-natural grassland, almost devoid of exotic species within about 20 years (O'Connor 2005). In brigalow systems, further research is needed on the succession of previously cultivated grasslands over longer time periods. In particular, information on time since cultivation is needed to provide guidance for the successful restoration of grassland communities. The rapid regeneration (recovery) of grassland communities shown in this and other studies is characterised by an increase in plant diversity in these formerly cropped agricultural lands.

4.4.4 Influence of spatial features and landscape context

Plant communities at local scales are influenced by their immediate environment and by colonisation of plants from surrounding areas (Federoff *et al*. 2005). In fragmented landscapes, matrix characteristics at different spatial scales have been shown to affect plant communities. In particular Roschewitz *et al*. (2005) showed that both landscape complexity (as measured by the percent of arable land) and farming system (organic or conventional) influenced local weed species diversity in German agro-ecosystems. Furthermore, Federoff *et al*. (2005) found that plant communities in French agro-ecosystems showed a significant response to both land-use type and landscape-use diversity (i.e. landscape context).

The structural and landscape variables examined in the regression analyses explained only a small, yet significant proportion of the variation in herbaceous plant species richness and cover. However, broad inferences can be made with respect to the hypothesis that spatial patterns of land use in the matrix affect locally sampled herbaceous vegetation communities. Regression analyses showed that local plant communities in both brigalow and the matrix were influenced more by remnant size and attributes of the surrounding landscape (landscape context) than by local structural features. This finding has implications for management and restoration of plant communities at local scales in agro-ecosystems, where consideration needs to be given to the composition and configuration of the surrounding landscape. The significance of these landscape context effects will be discussed more fully in Chapter 6.

4.5 Conclusions

Brigalow agro-ecosystems were found to support a diverse assemblage of native and exotic plant species that vary between different land management categories. In particular, there were significant differences in herbaceous plant species richness, cover and community composition between all land management categories along the intensification gradient, except uncultivated grasslands and previously cultivated grasslands. Brigalow systems contained the highest herbaceous plant species richness and cultivation the lowest, with total percentage of plant cover (excluding litter) highest in the grasslands. Hence, preservation of biodiversity should focus on the brigalow and grassland components of the landscape. Opportunities for enhancing biodiversity and restoring ecosystem function were evident in previously cultivated areas, where grassland plants showed signs of rapid regeneration.

There were no significant differences in plant species richness, herbaceous cover and community composition between core and edge in the same land management category, suggesting that adjacent land uses at the remnant/ matrix interface had no detectable influence on each other. This finding was unexpected, particularly for brigalow edges, where differences in community composition were expected due to the movement of propagules across land management boundaries. An explanation for this may be that the small brigalow patches sampled had the same levels of disturbance throughout.

Spatial patterns of land use in the surrounding landscape (landscape context) were found to exert a significant influence on locally measured plant species richness and cover. Hence, management and restoration efforts should consider not only local-scale habitat features, but also the spatial composition and configuration of the surrounding landscape.

CHAPTER 5

BIRD BIODIVERSITY AND AGRICULTURAL INTENSIFICATION

5.1 Introduction

Bird communities respond to changes in agricultural management that occur at a range of spatial and temporal scales (Saunders 1989; Chamberlain *et al*. 2000; Omerod and Watkinson 2000). Many studies have focussed on the response of bird species and communities in patches of remnant native vegetation to local-scale changes in vegetation structure and floristic composition (e.g. Loyn 1987; Mac Nally 1990; Farley *et al*. 1994), resource availability (Ford 1989), habitat patch size (Loyn 1987; van Dorp and Opdam 1987; Major *et al*. 2001) and land management (Opdam *et al*. 1985; Buckingham *et al*. 2006). Other studies have examined broader-scale influences such as the spatial pattern of the surrounding vegetation in the landscape (Mac Nally *et al*. 2000; Watson *et al*. 2000; Major *et al*. 2001; Bennett *et al*. 2006). More recently, studies have focussed on the composition and condition of the agricultural matrix surrounding vegetation remnants (landscape context) and their effects on bird communities (Bennett *et al*. 2004; Martin *et al*. 2006). The ability of different bird species to adapt to these local and landscape-scale habitat changes in both the short- and long-term has important implications for nature conservation and potentially ecosystem function in highly fragmented landscapes.

Bird species are affected in different ways by agricultural intensification, depending on various factors associated with their habitat requirements, population dynamics and behavioural characteristics (Opdam *et al*. 1985; Beier *et al*. 2002; Newton 2004). The general trend of decreasing bird species diversity with increasing land use intensity has been shown in studies both in Australia (e.g. Arnold *et al*. 1987; Martin *et al*. 2006) and overseas (Estrada *et al*. 1997; Petit *et al*. 1999; Donald *et al*. 2001; Woodhouse *et al*. 2005). For example, Arnold *et al*. (1987) found higher bird species diversity and different community composition in eucalypt/acacia woodland habitats than in more intensively managed open farmland in Western Australia. Martin and Catterall (2001) recorded generally fewer species in cane cropland than in patches of remnant heathland in eastern Australia. In addition to such reductions in species diversity, bird community and functional group composition can change from species of high conservation concern, to species of lower conservation significance (Aratrakorn *et al*. 2006). In southern Queensland, Martin *et al*. (2006) noted that clearing the tree layer in riparian habitat resulted in a complete transformation of the bird assemblage from a wide range of uncommon small-bodied species to a few large-bodied generalist foragers.

Within established agricultural matrices such as crops and pastures, bird assemblages have been shown to change in response to land management and gradients of intensification (Gregory *et al*. 2005). In particular, farmland bird populations and other taxa may decline in response to changes in land management such as grazing and tillage (Laiolo 2005; Woodhouse *et al*. 2005; Buckingham *et al*. 2006). For example, Laiolo (2005) found that farmland birds in Italy favoured less intensively managed habitats such as fallows, grasslands and winter stubbles over cultivated areas. Conversion to less intensive management (e.g. cropping to grazing land) has also been shown to benefit some bird species (Verhulst *et al*. 2004; Orlowski 2006), and may act to enhance the permeability (ability of species to move through the landscape) of matrix habitats, thereby improving landscape connectivity for other species, particularly those that are sensitive to fragmentation (Antongiovanni and Metzger 2005; Donald and Evans 2006).

Patches of remnant native vegetation in agricultural landscapes are typically affected by high levels of fragmentation and modification (McIntyre and Hobbs 1999). These patches may not provide suitable habitat for some of the more specialised native bird species that are sensitive to structural and micro-climatic changes associated with fragmentation, such as the creation of artificial (human-made) patch edges (Lovejoy 1986; Saunders *et al*. 1991; Murcia 1995; Stratford and Stouffer 1999). In small habitat remnants, these sensitive species may also be displaced at habitat edges by ubiquitous generalist species that use resources from the matrix to complement or substitute for those from natural habitats (Grey *et al*. 1998; Luck *et al*. 1999; Norton *et al*. 2000; Piper and Catterall 2004). For example, some studies have shown that levels of nest predation and parasitism are higher at patch edges compared with patch interiors (e.g. Paton 1994). Other studies in Australia show that bird assemblages may be greatly affected by other aggressive, competitive bird species such as the Noisy Miner (*Manorina melanocephala*) (Grey *et al*. 1998).

However, despite the absence of some of the more sensitive species, small remnants have been shown to provide important refuge and complementary habitat for a sub-set of the pre-fragmentation bird assemblage (Fischer and Lindenmayer 2002; Bennett *et al*. 2004). For example, Fischer and Lindenmayer (2002) found that 75% of all bird species predicted to be found in a fragmented landscape in southeastern Australia, were detected in remnant patches between 0.4 and 15.6 ha. Similarly, Johnson (2001) reported that most of the species recorded in the southern Brigalow Belt bioregion in 1885 have been reported in small fragmented remnants since the 1980s. These small habitat patches may also provide complementary resources for species that depend on larger patches, but can also move through the landscape (Fischer and Lindenmayer 2002). Some of these species may provide beneficial ecosystem services such as pest suppression in these landscapes (Jones *et al*. 2005).

Fragmented habitat conditions may also give rise to the colonisation, or an increase in the abundance of a suite of species favoured by broad-scale landscape modification (Loyn 1987; Hobbs and Saunders 1991; Barrett *et al*. 1994). The degree to which the bird assemblage resembles the original (i.e. pre-fragmentation) avifauna in remnant patches may depend on the size and condition of the patch (Watson *et al*. 2000; Major *et al*. 2001; Beier *et al*. 2002), and on the composition, connectivity and fragmentation of the surrounding landscape (McIntyre and Barrett 1992; Lindenmayer *et al*. 2003; Kupfer *et al*. 2006).

Island biogeography and metapopulation models have traditionally been used to explain extinction and colonisation in such fragmented agricultural landscapes, particularly in relation to patch size and distance to source populations (MacArthur and Wilson 1967; Hanski and Gilpin 1991). Under these theories, fragmented patches of native vegetation have been regarded as discrete islands, surrounded by an inhospitable matrix of homogeneous farmland that is of little or no value for biodiversity conservation (MacArthur and Wilson 1967). However, recent studies particularly in fragmented terrestrial environments such as agro-ecosystems, have suggested that as natural ecosystem components continue to diminish in extent and integrity, the composition and spatial configuration of the surrounding agricultural matrix of crops and grasslands may become important factors influencing the local occurrence of some bird species (Pearson 1993; Sisk *et al*. 1997; Brotons *et al*. 2005).

The type of land use surrounding a patch of native or semi-natural habitat can moderate the negative effects of isolation (Carroll *et al*. 2004), influencing both the composition of the bird assemblage it supports (Sisk *et al*. 1997; Lindenmayer *et al*. 2001), and the rates of dispersal and patch colonisation (Bender and Fahrig 2005). In a recent review, Kupfer *et al*. (2006) concluded that the mounting evidence for the influence of the matrix on biota in human-modified landscapes should prompt a shift in research efforts from patch-based examinations (e.g. patch area and distance metrics) to a landscape mosaic model (Forman 1995) that recognises the importance of different habitat components and gradients in the matrix.

The research focus on these 'landscape context' effects has revealed that biotic communities may be affected by a combination of local-scale habitat patch characteristics (e.g. habitat structural diversity, patch size) and by the nature and management of the surrounding landscape matrix (Mazerolle and Villard 1999; Fahrig 2001; Westphal *et al*. 2003; Yamaura *et al*. 2005). Some studies have shown that primarily local-scale habitat factors have a strong influence on bird communities (Major *et al*. 2001; Watson *et al*. 2000; Herzog and Kessler 2006). Other studies have shown that bird communities may be affected by factors at a range of different spatial scales (Pearson 1993; Bennett *et al*. 2004). In particular, Martin *et al*. (2006) showed that 80% of bird species in riparian habitats in grassy woodlands of southeastern Queensland were influenced by a combination of local riparian habitat condition and landscape context factors, and that a number of species that were found in riparian sites surrounded by woodland declined or were absent in sites surrounded by cleared pasture lands or cropping.

In the temperate eucalypt woodland habitats of south-eastern and south-western Australia, many bird species are declining in response to local-scale habitat loss and wider scale habitat fragmentation (Saunders 1989; Barrett *et al*. 1994; Reid 1999; Fisher 2000) and modification such as livestock grazing (Jansen and Robertson 2001; Martin and Possingham 2005). A similar decline has been documented in the northern Brigalow Belt bioregion (Woinarski and Catterall 2004; Woinarski *et al*. 2006), where broad-scale habitat fragmentation has occurred more recently (Wilson *et al*. 2000). However, few studies on the effects of fragmentation on birds have been conducted in the southern Brigalow Belt bioregion of Queensland. Indeed, few Australian studies have compared bird assemblages in fragmented vegetation patches with those in the surrounding agricultural matrix of grassland and cropping (but see Arnold *et al*. 1987; Martin *et al*. 2006). Furthermore, a comprehensive review of the literature has revealed that no other Australian studies have investigated the impacts of landscape context on birds that inhabit the agricultural matrix of grassland and cropping.

This study asks the general question, does the diversity and composition of bird communities, sampled at the local scale, differ along a gradient of agricultural intensification from remnant vegetation to frequently cultivated land? The research also identifies whether bird communities are influenced by local habitat attributes and/or by the composition and spatial configuration of the surrounding matrix of grassland and cropping land.

More specifically, this study examines the hypotheses that:

1) Bird community diversity and composition change as land use intensifies;
2) Habitat complexity of the vegetation and the spatial configuration of the surrounding landscape both influence bird communities in vegetation remnants and in the agricultural matrix.

The effect of edges was not examined for birds because most of the sampled Brigalow remnants were considered too small to contain core areas that would be relevant for mobile vertebrates.

5.2 Methods

5.2.1 Experimental design

Briefly (as described more fully in Section 2.3), the study area was divided into the following four broad land management categories, according to past and current land-use practices:

1) Remnant brigalow vegetation that has never been cleared (Brigalow, n = 20);
2) Grassland that has not been cultivated following clearing of the original brigalow vegetation (Grass$_U$, n = 3);
3) Grassland that has been previously cultivated but left fallow for 3-15 years (Grass$_P$, n = 4);
4) Recently (<2 yrs) cultivated land (Cultivation, n = 13) (Figure 2.5).

A 200 x 100 m belt transect was established at Brigalow core (BC) and matrix core (MC) at each study site, parallel to the remnant edge. The same pair of fixed transects at each study site was used for all bird surveys and assessments of habitat complexity. Unlike soil carbon and plant communities, which were sampled at the edge and core of each site (see Figure 2.6), birds were sampled only at Brigalow core and matrix core because of constraints of remnant patch size, overlapping sampling areas and the highly mobile nature of birds.

5.2.2 Bird surveys

Bird surveys were conducted from late spring to early autumn (October 2002 to March 2003), between one and four hours after sunrise in fine, calm weather conditions. This sampling period was chosen to coincide with the high levels of bird activity during and after breeding season, and with visiting annual summer migrants to the region (Whitmore *et al*. 1983). Sampling methods were restricted by the size of Brigalow remnant study sites (smallest patch was 2.10ha). Transects within each study site were surveyed three times, with repeat surveys conducted on different days during the sampling period. Sampling duration (20 min) and the area covered (i.e. 2 hectares) were consistent with the methods used in the Atlas of Australian Birds project (Barrett *et al*. 2003). During surveys, all birds seen or heard within the transect boundaries were recorded; however, birds flying more than 5m above the vegetation in Brigalow and more than 5m above the ground in matrix sites were not recorded in formal survey data. Three observers were used to collect bird data, following an initial period of training to coordinate survey methods and to ensure consistency and accurate species identification.

To determine optimum sampling efficiency (i.e. the number of surveys needed to detect the maximum number of bird species per site), a stopping rule for the number of surveys was determined using data from Brigalow and matrix surveys at five pilot study sites (pilot sites were 1, 2, 3, 4 and 9). Based on permuted data for 5 surveys from each site, the mean average increase in species richness per survey, across the five pilot sites, was determined (Appendix 8). Based on these preliminary data, a stopping rule was applied when the mean increase of new species per survey fell below 2, which occurred after 3 surveys. Based on these findings, the remaining sites were surveyed three times, with only the first three of the surveys from the pilot analysis used in the subsequent analyses. Preliminary winter surveys using the methods described above were also conducted from June-July 2003. Three surveys were conducted in the Brigalow and matrix at sites 1, 2, 3, 4 and 9. All of the bird species recorded during winter sampling had already been observed in summer. Based on these results, no further winter surveys were conducted in the remaining sites and data from preliminary winter surveys were not included in the analyses.

Some studies have shown that annual variation can have a significant influence on species composition (e.g. Maron *et al*. 2005). However, sampling of birds during a single year was considered to be sufficient for testing the hypotheses of this research. In particular, my focus was on determining relative differences in bird richness, diversity and community composition between broad land management categories at the time of sampling, independent of annual or seasonal variation.

5.2.3 Habitat complexity

The structural characteristics of the vegetation were assessed within the transects at Brigalow core and matrix core. Visual estimates of percent cover of vegetation strata and groundcover components were made in each transect by the same observer between March and April 2004. Subjective estimates of the percentage of tree canopy cover (>20 m, 10-20 m and <10 m in height), shrubs (>2 m, 1-2 m and <1 m), forbs and herbs (<0.5 m), grasses, bare ground, litter (including attached dead herbaceous plant material) and logs (>10 cm diameter) were made within each transect (after Catling and Burt 1995).

5.2.4 Patch size and landscape information

As described in more detail in Section 2.3.4 of the general methods, spatial information was derived using aerial photographs captured in 2001 and geo-referenced using GIS software (ArcView 3.1). Landscape context variables were calculated for each site, by summing the total area of Brigalow vegetation, grassland (including Grass_U and Grass_P) and cultivation within 500 m, 1000 m, 1500 m and 2000 m radii around Brigalow remnants at each study site. Mean patch size (MPS) and number of patches (NumP), were also derived for each land management category at each distance (Appendix 1).

5.2.5 Statistical analyses

All bird species recorded during formal surveys were included in the analyses. Cumulative bird species richness and total abundance from three surveys at each site were used in analyses. Summed bird abundance gave an index of the intensity of use of each site by each bird species (Martin and Catterall 2001; Martin *et al.* 2006). Species richness data was log transformed to meet the assumptions of parametric tests (Sokal and Rohlf 1995). Environmental variables were inspected for normality, and transformed where appropriate. Percentage cover data of vegetation structural attributes were arcsine square root transformed prior to analyses.

Two measures were used to represent bird diversity; species richness (S = number of species) and the Shannon index of diversity ($H' = -\sum p_i \ln p_i$), where p_i is the proportion of individuals found in the i^{th} species (see Shannon and Weaver 1948; Greig-Smith 1983; Carr 1996). Mean species richness, total abundance and Shannon diversity were compared across matrix land management categories using one-way analysis of variance (ANOVA), with *a priori* contrasts ($\alpha = 0.05$). These analyses were performed with both the omission and inclusion of a potential outlier (site 12) from the 'Uncultivated grassland' ($Grass_U$) category, giving different results. The results presented here are those from analyses excluding the outlier; however, these analyses will be interpreted conservatively because of low sample size in the $Grass_U$ category (n=2). One-way ANOVA, with *a priori* contrasts ($p<0.05$) was used to compare differences in total species richness, abundance and diversity between Brigalow, uncultivated grassland ($Grass_U$), previously cultivated grassland ($Grass_P$) and Cultivation sites.

Bird species were assigned to foraging guilds (functional groups), following the guild classification system developed by Recher and Holmes (1985) and adapted for bird communities in fragmented Brigalow systems, based on observed foraging behaviour (Appendix 9). Due to a less diverse species assemblage in remnant Brigalow sites, some of the guilds used by Recher and Holmes (1985) and by Ford (1989) (e.g. bark foraging insectivores) are not represented in this study. Non-parametric analyses (Chi-square tests) were performed on functional group data because these data did not meet the assumptions of parametric tests. Residual values were used to determine which groups showed higher or lower than expected abundance in different land management categories (Moore and McCabe 1999).

Patterns in overall bird community composition between land management categories (using all data, including site 12) were investigated using multivariate analysis procedures in PRIMER 5 (Clarke and Warwick 2001). Ordination was performed using non-metric multi-dimensional scaling (nMDS), based on the Bray-Curtis similarity measure, with analysis of similarity (ANOSIM) used to determine whether site types differed significantly on the basis of their bird assemblages. Similarity percentage analysis (SIMPER) was used to determine which species contributed most to the dissimilarity between significantly different land management categories. These multivariate methods, developed by Clarke (1993) for marine systems, are increasingly being used for bird studies in Australia (see Watson *et al*. 2000; Major *et al*. 2001; Antos and Bennett 2005; Maron *et al*. 2005; Antos *et al*. 2006).

One-way ANOVA was used to compare habitat complexity variables that were recorded in two or more land management categories. Ordination (nMDS), combined with ANOSIM and SIMPER were used to compare overall habitat complexity across different land management categories.

Species richness, total abundance and Shannon diversity were modelled as a function of environmental (habitat complexity and landscape) parameters using the stepwise multiple linear regression procedure in SPSS version 12.0.1 (SPSS Inc. 2003). Prior to the regressions, highly correlated habitat and landscape variables were excluded (Appendix 3), leaving a more parsimonious set of variables for the analyses (Dauber *et al*. 2003) (Table 5.1). This data reduction procedure means that inferences are restricted to groups of environmental data (e.g. habitat or landscape), rather than about specific environmental variables. Noisy Miners abundance was included as an explanatory variable because of its noted effects on woodland bird communities (Grey *et al*. 1998).

Table 5.1. Habitat and spatial explanatory variables used in the stepwise regression models, following removal of highly correlated variables. Habitat biotic variables were different for the separate Brigalow and matrix analyses, but the same spatial/ landscape context variables were included in both analyses

Brigalow	Matrix
Habitat (% cover)	**Habitat (% cover)**
Trees 10-20m cover	Herbs & forbs cover
Shrubs >2m cover	Bare ground cover
Grasses cover	Litter cover
Herbs & forbs cover	
Logs cover	
Noisy Miner abundance	
Spatial	**Spatial**
Patch Area	Patch Area
Grassland area 500m	Grassland area 500m
Number Grassland patches 500m	Number Grassland patches 500m
Brigalow area 2000m	Brigalow area 2000m
Grassland area 2000m	Grassland area 2000m
Number Brigalow patches 2000m	Number Brigalow patches 2000m

5.3 Results

5.3.1 General bird community information

A total of 54 bird species was recorded across all land management categories during formal surveys. These and all other species recorded outside formal survey areas during sampling (total of 84 species) are listed in Appendix 9. Of the species recorded in formal surveys, only two species were exotic (Common Starling and Indian Myna), four were birds of prey (Australian Kestrel, Black-shouldered Kite, Brown Falcon and Spotted Harrier), one species was nocturnal (Tawny Frogmouth) and two species were waterbirds (White-faced Heron, Straw-necked Ibis). Other well-represented groups were parrots (7 species) and honeyeaters (5 species). One species, the Painted Honeyeater, is listed nationally as 'near threatened' (Garnett and Crowley 2000) and is considered to be rare in Queensland (Sattler and Williams 1999). This species was recorded in 3 of the Brigalow sites during formal surveys and in various other locations throughout the study landscape.

Twenty-four species (44%) were recorded only in Brigalow sites and 12 species (22%) were recorded only in the matrix. The remaining 18 species (33%) were recorded in both Brigalow and matrix sites (Appendix 9). The most common species in Brigalow remnants were Crested Pigeon, Noisy Miner and Cockatiel, found in 20, 18 and 17 of the 20 study sites respectively. Thirteen other species were recorded in more than 10 of the Brigalow sites (Appendix 9). The most common species in the matrix sites were Australian Magpie, Torresian Crow and Crested Pigeon, found in 16, 13 and 8 sites respectively. Species recorded only in Cultivation included Black-shouldered Kite, Brown Quail, Peaceful Dove, Straw-necked Ibis and Spotted Harrier. Five species, Australian Magpie, Indian Myna, Pied Butcherbird, Torresian Crow and Galah were recorded in at least one site in each land management category.

There were significant differences between land management categories for bird species richness (F = 67.473, $p<0.001$), total abundance (F = 52.672, $p<0.001$) and Shannon diversity (F = 53.806, $p<0.001$). Species richness, abundance and Shannon diversity were significantly higher in Brigalow sites than in any of the other land management categories (*a priori* contrasts $p<0.05$, Figure 5.1). Within the matrix land management categories, bird species richness and Shannon diversity were significantly higher in Grass_U sites than in Grass_P and Cultivation sites (*a priori* contrasts $p<0.05$). There were no significant differences between total abundance in any of the matrix land management categories (Figure 5.1).

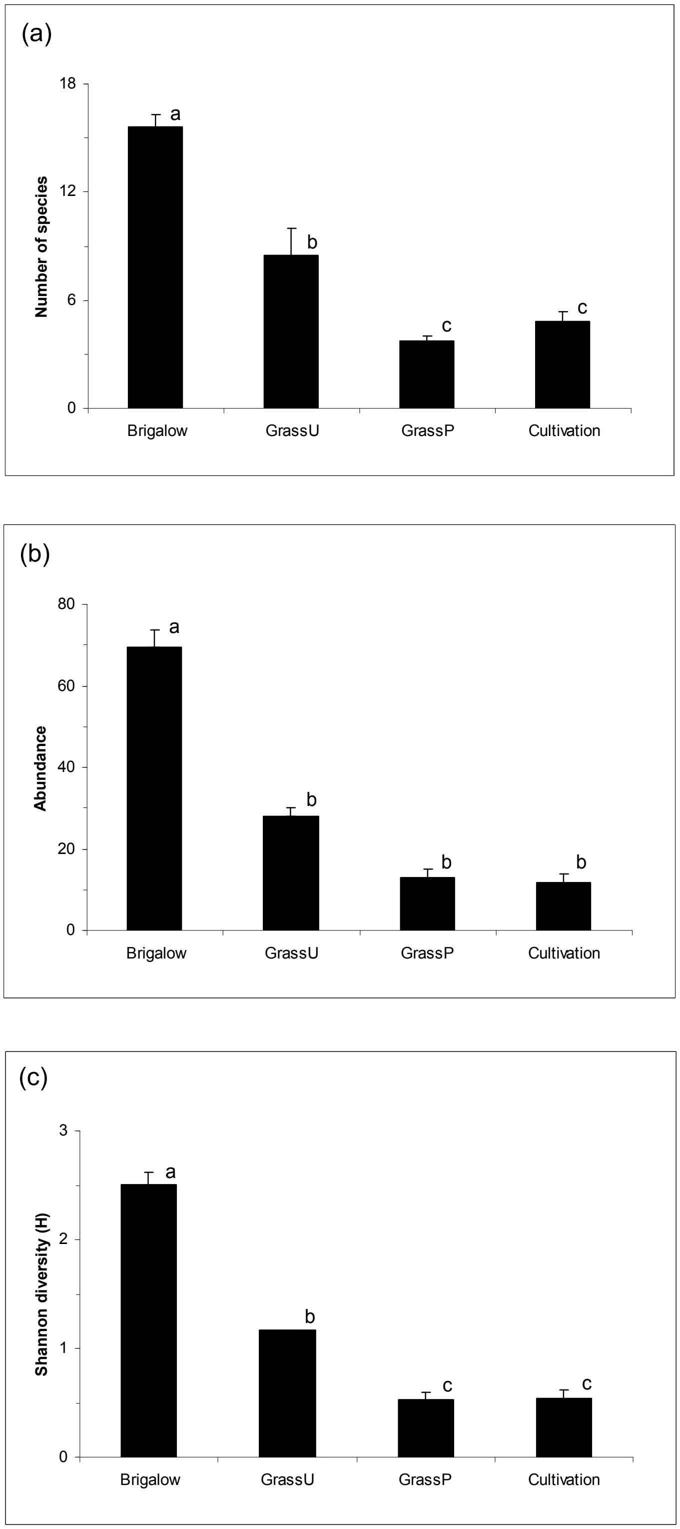

Figure 5.1. Mean (± 1 standard error) values for bird a) species richness, b) total abundance and c) Shannon diversity (H) in Brigalow, uncultivated grassland (Grass_U), previously cultivated grassland (Grass_P) and current cultivation (Cultivation). Means sharing the same letter are not significantly different (*a priori* contrasts p>0.05). Error bars are standard errors.

5.3.2 Functional groups / foraging guilds

A greater number of functional groups was recorded in Brigalow sites than in any of the other land management categories. Seven of the eight functional groups were recorded in Brigalow sites, compared with three in Grass_{U} sites, four in Grass_{P} sites and four in Cultivation sites (Table 5.2). Canopy-foraging insectivores, frugivores and understorey species were recorded only in Brigalow sites. Ground-foraging insectivores and granivores were the dominant functional groups in all land management categories (Table 5.2). More than fifty percent of all birds recorded in the matrix land management categories were ground-foraging insectivores. Raptors were proportionally highest in Cultivation sites.

There was a highly significant difference ($\chi^2 = 133.93$, $p<0.001$) in distributions across the land management categories due mainly to the higher than expected proportions of ground-foraging insectivores in both grassland and cultivation categories and a higher than expected proportion of raptors in the cultivation sites (Table 5.2).

Table 5.2. Proportion of bird functional groups in each land management category. Columns sum to 100 percent.

%	Brigalow	Grass_{U}	Grass_{P}	Cultivation
Ground-foraging insectivore	32.7	57.8	71.2	58.3
Raptor	0.4	0	0	5.3
Granivore	42.1	42.2	15.4	30.5
Canopy-foraging insectivore	1.7	0	0	0
Open grassland species	0	0	13.5	6.0
Nectarivore/insectivore	15.7	0	0	0
Frugivore	4.0	0	0	0
Understorey insectivore	3.4	0	0	0

5.3.3 Bird community composition

An nMDS ordination of avian abundance data showed a distinct separation of Brigalow and matrix sites (Figure 5.2). Bird community composition displayed a high amount of variability within the matrix (Figure 5.2).

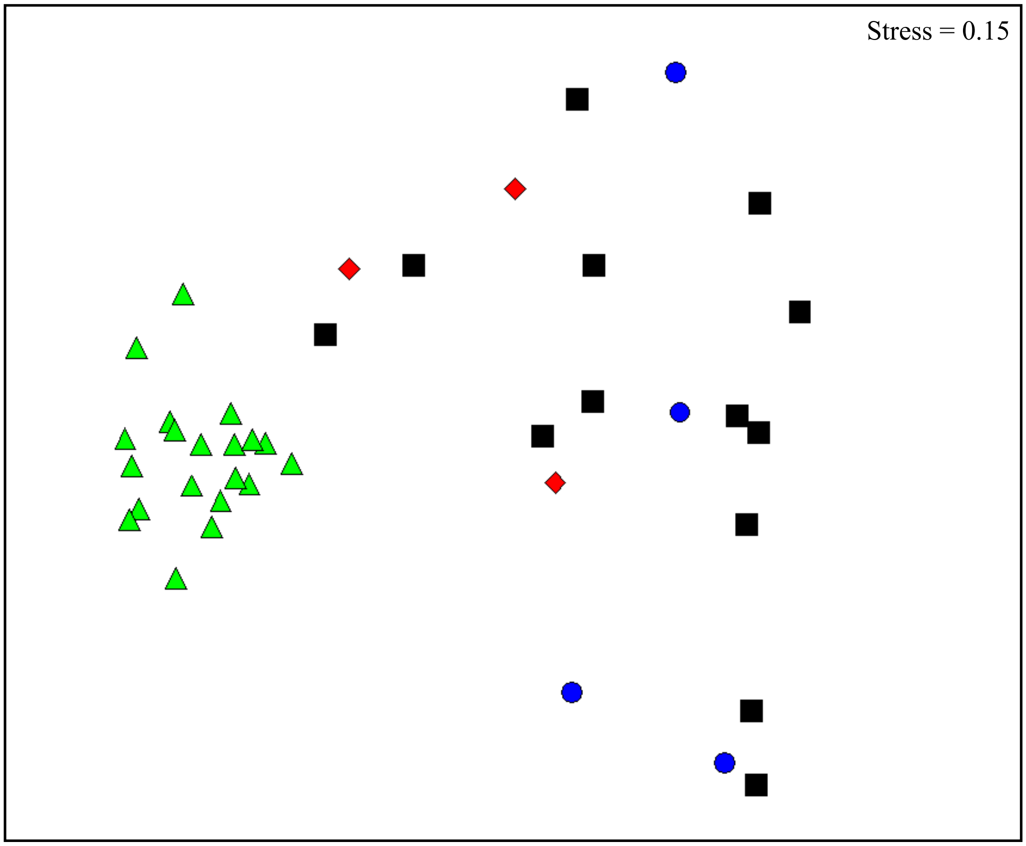

Figure 5.2. Two-dimensional ordination (nMDS) of bird abundance data showing each land management category. ▲ = Brigalow, ♦ = $\mathrm{Grass_U}$, ● = $\mathrm{Grass_P}$, ■ = Cultivation.

One-way Analysis of Similarity (ANOSIM) showed significant differences in bird community composition among land management categories (Global $R = 0.791$, $P < 0.001$). Pairwise tests showed significant differences ($P < 0.05$) between Brigalow and all other land management categories, but there was no significant effect of land management category on bird community composition among matrix sites (Table 5.3).

Table 5.3. Summary of Analysis of Similarity (ANOSIM) on bird abundance data. Values are R statistics (from pairwise tests) with significance level indicated (Global R = 0.791, Sign level < 0.01)

	Brigalow	**$GRASS_U$**	**$GRASS_P$**
$GRASS_U$	0.966*	1	-
$GRASS_P$	0.973**	-0.074^{ns}	1
Cultivation	0.844**	0.05^{ns}	0.153^{ns}

**p < 0.001, *p < 0.05, ns = not significant

A similar suite of bird species contributed to a large proportion of the dissimilarity between Brigalow and the three matrix land management category sites (Table 5.4). In particular, the high abundance of the Noisy Miner, Crested Pigeon and Cockatiel in Brigalow sites, accounted for a large proportion of the dissimilarity between Brigalow and matrix samples (Table 5.4).

Table 5.4. Average dissimilarity between land management categories (LMC) and the average abundance of bird species that contributed up to 50% of the dissimilarity between LMCs. Species are listed in decreasing order of their importance in discriminating the two sets of samples.

Species	**Average abundance**		**Cumulative %**
Average dissimilarity = 87.89	**Brigalow**	**Cultivation**	
Noisy Miner	7.75	0.00	11.49
Crested Pigeon	8.10	1.62	22.26
Cockatiel	7.50	0.54	32.08
Grey Butcherbird	4.50	0.15	38.58
Red-rumped Parrot	5.20	0.54	44.96
Apostlebird	4.25	0.46	51.08
Average dissimilarity = 79.05	**Brigalow**	**GrassU**	**Cumulative %**
Noisy Miner	7.75	0.33	10.85
Cockatiel	7.50	0.00	20.73
Crested Pigeon	8.10	3.33	28.80
Red-rumped Parrot	5.20	0.67	34.98
Grey Butcherbird	4.50	0.33	41.14
Apostlebird	4.25	0.00	47.15
Indian Myna	1.75	2.67	51.67
Average dissimilarity = 92.02	**Brigalow**	**GrassP**	**Cumulative %**
Crested Pigeon	8.10	0.00	11.37
Noisy Miner	7.75	0.00	22.17
Cockatiel	7.50	0.00	31.60
Grey Butcherbird	4.50	0.00	37.92
Red-rumped Parrot	5.20	0.00	43.89
Apostlebird	4.25	0.00	49.65
Galah	4.20	1.50	54.91

Average abundance represents the average number of birds recorded per plot within each land management category. Cumulative % represents the cumulative influence of the variables to the overall Bray-Curtis dissimilarity.

5.3.4 Habitat complexity

Trees of all height classes, shrubs >2m, shrubs 1–2m and logs were found only in Brigalow sites, with low numbers of shrubs under 1m in only two of the sampled grassland areas (Table 5.5). Four of the measured structural attributes (forbs and herbs, grasses, bare ground and litter) were common to all land management categories. Brigalow sites had the highest cover of forbs and herbs (18%) and litter (35%). The cover of grasses was high in uncultivated (82%) and previously cultivated grasslands (74%). The proportion of bare ground was highest in cultivated sites (63%) (Table 5.5).

Table 5.5. Mean percent cover *(±1 standard error*) of habitat variables for each land management category. Results of contrasts are indicated by superscripts. Values with the same letter are not significantly different ($p<0.05$).

	Brigalow (n=20)	**GrassU (n=3)**	**GrassP (n=4)**	**Cultivation (n=13)**	**F**	**P**
Trees>20m	5.5 (1.3)	0.0	0.0	0.0	-	-
Trees10-20m	9.3 (1.2)	0.0	0.0	0.0	-	-
Trees<10m	6.7 (3.0)	0.0	0.0	0.0	-	-
Shrubs>2m	17.2 (3.2)	0.0	0.0	0.0	-	-
Shrubs1-2m	6.8 (1.9)	0.0	0.0	0.0	-	-
Shrubs<1m	4.7 (1.2)^a	0.7 (0.7)^b	0.3 (0.3)^b	0.0^b	3.079	0.04
Forbs/ herbs	18.0 (2.2)^a	4.0 (1.0)^b	4.5 (0.9)^b	3.15 (0.8)^b	20.704	0.00
Grasses	27.4 (3.0)^a	81.7 (8.3)^b	74.3 (3.6)^b	36.0 (8.9)^a	17.797	0.00
Bare ground	15.3 (2.3)^a	9.67 (7.8)^a	15.5 (4.9)^a	62.5 (6.7)^b	22.308	0.00
Litter	35.4 (3.9)^a	6.3 (1.9)^b	6.3 (1.8)^b	17.8 (5.2)^b	9.501	0.00
Logs	5.45 (0.6)	0.0	0.0	0.0	-	-

An nMDS ordination of habitat complexity data showed a clear separation of Brigalow and matrix land management categories (Figure 5.3). A gradient in habitat complexity is evident on the ordination from Brigalow sites (on the left of the diagram) to grassland (Grass_U and Grass_P) and cultivation sites on the right. Grassland and Cultivation sites were also generally well separated (Figure 5.3).

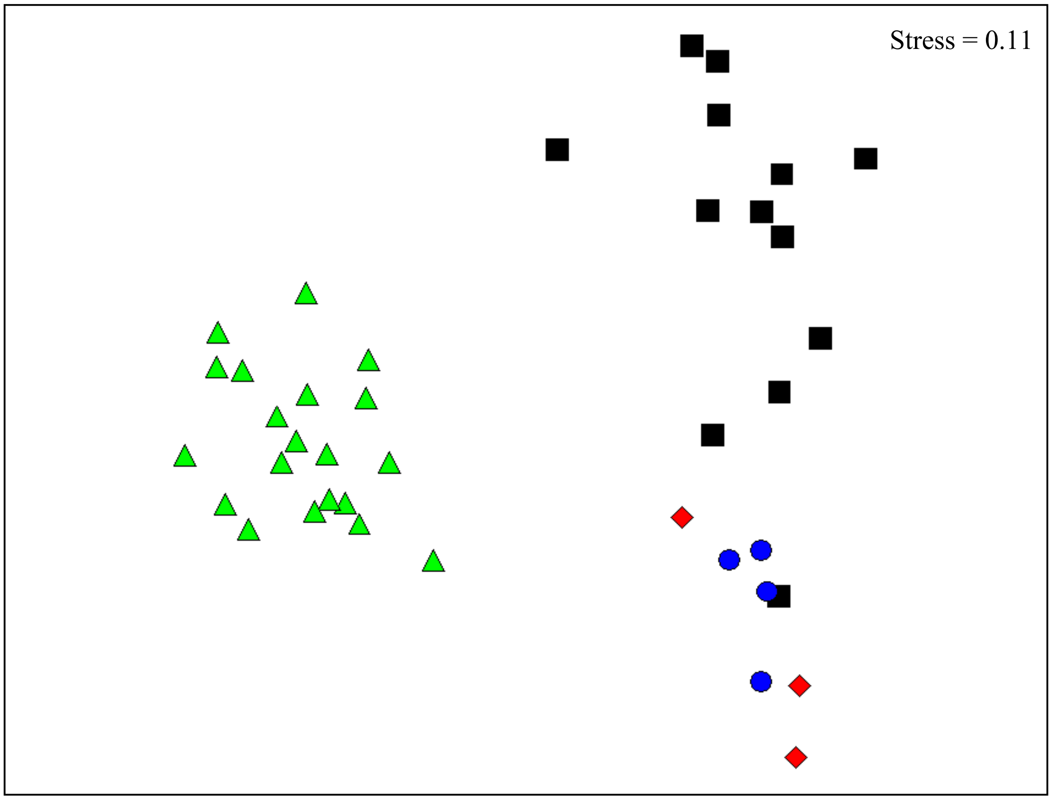

Figure 5.3. Two-dimensional ordination (nMDS) of % cover data of habitat complexity showing each land management category. ▲= Brigalow, ♦ = Grass_U, ● = Grass_P, ■ = Cultivation.

One-way ANOSIM showed significant differences in habitat complexity between land management categories (Global $R = 0.874$, $p = 0.001$). Pairwise tests showed significant differences in habitat complexity ($p < 0.05$) between all land management categories except between uncultivated grassland (Grass_U) and previously cultivated grassland (Grass_P) ($p>0.05$) (Table 5.6).

Table 5.6. Summary of ANOSIM on percent cover of habitat complexity data. Values are R statistics (from pairwise tests) with significance level indicated (Global R = 0.874 Sign level = 0.001)

	Brigalow	$GRASS_U$	$GRASS_P$
$GRASS_U$	0.966^{**}	1	-
$GRASS_P$	0.995**	-0.037^{ns}	1
Cultivation	0.966**	0.583*	0.451*

**p < 0.001, *p < 0.05, ns = not significant

SIMPER analyses (Appendix 10) showed that grass cover contributed most to the dissimilarity in all comparisons, except between Brigalow and Cultivation, where higher cover of bare ground in cultivated sites contributed most to the dissimilarity. The absence of trees and shrubs in matrix sites contributed to much of the dissimilarity between Brigalow and all three matrix land management categories. Dissimilarities between land management categories in the matrix were largely due to differences in grass and litter cover (Appendix 10).

5.3.5 Influence of habitat complexity and landscape pattern on bird species richness, diversity and abundance

A combination of patch and landscape-scale variables explained a significant amount of the variance in the species richness within Brigalow remnants (Table 5.7). In particular, the area of Brigalow within a 2000 m radius of the study site, and percentage log cover at a local scale were significant explanatory variables, explaining 40% of the variance for species richness in these sites. Percentage cover of grasses alone explained a maximum of 17% variance in total bird abundance in Brigalow sites. There were no significant landscape or patch-scale predictor variables for Shannon diversity of birds in Brigalow (Table 5.7).

Fifty-six percent of the total variance in species richness in matrix sites was explained by the area of the adjacent Brigalow patch and the number of grassland patches at the 500 m scale (Table 5.7). There were no significant landscape or patch-scale predictor variables for abundance or Shannon diversity of birds in the matrix (Table 5.7). Noisy Miner abundance failed to explain a significant amount of the variance for any of the tested variables.

Table 5.7. Summary of habitat models generated by multiple linear stepwise regression for the dependent variables bird species richness, abundance and Shannon Diversity in Brigalow and matrix sites.

Dependent variable	Explanatory variables in final model	d.f.	Adjusted R^2	*F*	*B (s.e.)*	*P*-value
Brigalow sites						
Species richness	Brigalow 2000 m	1,19	0.23	6.70	-1.44 (0.45)	0.019
	Brigalow 2000 m + Logs	1,19	0.40	7.29	0.60 (0.25)	0.005
Abundance	Grass Cover	1,19	0.17	4.94	58.66 (26.41)	0.039
Shannon Diversity	No variables significant					
Matrix sites (Grass$_U$ + Grass$_P$ + Cultivation)						
Species richness	Patch Area	1,19	0.37	11.97	0.52 (0.10)	0.003
	Patch Area + Number of Grassland patches at 500 m	1,19	0.56	13.01	-0.01 (0.00)	0.000
Abundance	No variables significant					
Shannon Diversity	No variables significant					

Analyses included patch-scale habitat and spatial variables. Species richness data log (x+1) transformed, percent cover data arcsine-root transformed. Analyses were performed for each habitat and spatial variable, but only significant results ($p<0.05$) are displayed. B = unstandardised coefficient, with standard error. Model R^2 values are cumulative adjusted coefficients of determination for the entire regression equation

5.4 Discussion

Despite high levels of fragmentation and modification, small patches of brigalow vegetation and the surrounding agricultural lands continue to provide suitable habitat for a diverse assemblage of native bird species. Forty-four percent of bird species were recorded only in Brigalow remnants and 78% of species were recorded in Brigalow and at least one other land management category. The richness, abundance and diversity of these species were all significantly higher in Brigalow remnants than in the adjacent matrix of cropping and grassland. Within the matrix, species richness and diversity were higher in uncultivated grasslands than in current cultivation or previously cultivated grasslands, despite there being no differences in habitat complexity detected between the two grassland categories. The composition of the bird community in Brigalow sites was different from that in all of the three matrix land management categories, but there were no differences in bird community composition between any of the matrix categories. The species richness of birds in Brigalow sites was explained by a combination of site and landscape context variables, while richness in matrix sites was explained by a combination of adjacent remnant patch size and landscape context. Local habitat was the only significant predictor of total bird abundance in Brigalow sites.

5.4.1 Avian assemblages in Brigalow remnants

There are limited published studies on bird biodiversity in brigalow habitats. Those studies that have examined brigalow bird communities (e.g. Whitmore *et al*. 1983; Leach and Hines 1993; Dorricott *et al*. 1998; Popple and Date 1998) found a similar assemblage of bird species in Brigalow remnants to the present study. Furthermore, many of the species found to occur in other native vegetation associations (e.g. eucalypt and bull oak habitats) in studies from southern regions of Australia (see Reid 1999; Major *et al*. 2001; Barrett *et al*. 1994; Watson *et al*. 2000), were also recorded in the present study. However, many of the rarer species from these southern landscapes were not recorded in my Brigalow sites. For example, only three of the 20 species recognised by Reid (1999) as declining in the Sheep-Wheat zone of New South Wales (Grey-crowned Babbler, Rufous Whistler and Restless Flycatcher) were represented in low numbers in this highly fragmented brigalow landscape. This may reflect the association of many of these declining species with non-brigalow habitat types as well as their more southerly distribution (Johnson 2001). Only one of the seven species nominated by McFarland *et al*. (1999), as being priority species for conservation planning in the Brigalow Belt South bioregion (Painted Honeyeater), was recorded in my study sites.

Johnson (2001) proposed that avifaunal assemblages in brigalow vegetation communities are a subset of a wider forest and woodland fauna, with bird species found in Brigalow, also found in eucalypt forest and woodlands. For example, there are no bird species that are endemic to brigalow communities and those species that have been lost from the Brigalow Belt bioregion have been birds of eucalypt woodlands, rather than brigalow forests. These characteristics have also been proposed as a reason for the apparent resilience of brigalow bird communities at a regional level. In particular, Johnson (2001) found little difference between current bird species lists for the Brigalow Belt South bioregion and the bird assemblage observed by Broadbent (1885), prior to significant agricultural development. Across the bioregion, most of these species remain common, despite a long history (50 years) of broad-scale mechanical clearing, suggesting a possible tolerance to habitat fragmentation compared with southern woodland species (Johnson 2001).

However, unlike the resilience suggested by bird communities at a regional scale, several bird species were conspicuously absent from the brigalow patches in this study. For example, some species that are reported to be common in larger patches of similar brigalow/belah vegetation elsewhere in the southern Brigalow Belt bioregion, were not found or were in very low abundance, in the Brigalow study sites. In particular, small insectivorous species such as Rufous Whistler, Eastern Yellow Robin, Grey Shrike-thrush, White-browed Treecreeper and Striated Pardalote are among the most common species in the brigalow/belah associations of Southwood National Park (7120 ha), 150 km to the south-west of my study area (Maron, M. 2006, pers. comm. 11 Apr.). Some of these species have been shown to decline in response to landscape fragmentation and modification in other studies (e.g. Grey *et al*. 1997; Reid 1999; Woinarski *et al*.

2006) and are therefore considered to be of higher conservation significance (Reid 1999); they also play a role in maintaining woodland functions such as insect predation and tree health (Grey *et al*. 1997; Recher and Majer 2006). Woinarski *et al*. (2006) showed a decline in Rufous Whistler, Grey Shrike-thrush and various other species in response to extensive land clearance in central Queensland. Other unpublished studies have found higher occupancy of these and other small, insectivorous species in fragmented Brigalow remnants of similar size closer to the study area (Johnson 2001; Bowen, M. 2006, pers. comm., 7 Apr.). In particular, some of these species were recorded in a recent survey of bird communities in fragmented brigalow and other vegetation remnants in close proximity (50 km) to the sampled sites in this study (Ford, G. 2006, pers. comm., 10 Apr.). It is possible then, that these species once occupied my study sites, but that habitat fragmentation and disturbance associated with surrounding management practices and edge effects (Murcia 1995) may have lead to their local decline in the study area. These species may also have been absent because of the dry conditions during the sampling period.

Another possible explanation for the absence or low abundance of various small insectivorous birds from the study landscape was the influence of Noisy Miners in the majority of sampled Brigalow patches. Noisy Miners have been shown to display indiscriminate interspecific aggression and exclusion of other bird species from vegetation patches (e.g. Loyn 1987; Grey *et al*. 1997). Furthermore, clear relationships have been shown between vegetation type, remnant area and bird species distributions and the presence of Noisy Miners (Loyn 1987; Grey *et al*. 1997, 1998). The richness of small woodland bird species is also negatively associated with Noisy Miners in small <20 ha (Loyn 1987; Ford *et al*. 1995; MacNally *et al*. 2000; Piper and Catterall 2004) and even large >200 ha (Major *et al*. 2001) remnants. Although the effect of the presence or absence of Noisy Miners could not be meaningfully tested in the present study due to miners inhabiting all but two of the sites, results showed that the variation in richness and diversity of bird assemblages in Brigalow was not significantly explained by the relative abundance of Noisy Miners.

Links between habitat degradation and low structural diversity, and high abundance of Noisy Miners have also been shown (Grey *et al*. 1998). However, despite the high cover of a structurally diverse shrub layer (>20%), dominated by Wilga (*Geijera parviflora*) in the majority of the sampled Brigalow sites (refer Table 5.5), Noisy Miner abundance remained high. This observation may have been caused by the high edge to area ratio of the Brigalow study sites.

Regardless of the exact mechanisms behind loss of some functional groups, the bird communities found in Brigalow remnants in the study landscape conform to the patterns of 'biotic homogenisation' described by McKinney and Lockwood (1999), with a decline in species richness and the replacement of species of high conservation significance (e.g. small, canopy-foraging insectivorous species) with species of lower conservation significance (e.g. medium-large ground-foraging insectivores). The reduced bird assemblage, particularly the decline in small insectivorous bird species, may have significant implications for ecosystem functions such as maintaining vegetation condition through predation of foliage-feeding insects (Grey *et al*. 1997; Recher and Majer 2006). However, despite their depauperate avifauna, these small fragmented patches are all that remains of lowland brigalow associations throughout much of the southern Brigalow Belt bioregion. This study shows that they have significantly higher levels of bird diversity than the surrounding agricultural matrix and therefore contribute significantly to overall landscape biodiversity and ecosystem function.

5.4.2 Land management categories and bird assemblages

Bird assemblages in the more floristically diverse (Section 4.3) and structurally complex remnant brigalow vegetation (Table 5.5) displayed predictably higher abundance and species richness, and were different in community composition than bird communities in any of the grassland and cropping land management categories in the matrix. Other studies have also shown lower species richness in highly modified habitat such as grassland and cultivation, compared with more structurally diverse remnant vegetation (Arnold *et al*. 1987; Martin and Catterall 2001; Woodhouse *et al*. 2005). For example, Arnold *et al*. (1987) recorded 25 bird species in woodland and 11 species in open farmland in eucalypt/acacia woodland in Western Australia, but did not differentiate between crop and pasture in the matrix.

However, not all agricultural practices have negative effects on bird communities. The majority of birds recorded in the small brigalow patches in this study were generally ubiquitous in the landscape and of low conservation significance; consisting of species that have expanded their distributions and increased in abundance in response to habitat fragmentation and land use change (Barrett *et al*. 2003). The abundance of a few medium to large-bodied generalist species, including many of the most common species found in the brigalow study sites (e.g. Crested Pigeon, Australian Magpie, Torresian Crow and Noisy Miner), have been shown to increase in vegetation patches surrounded by intensive agricultural land uses in other studies (e.g. Loyn 1987; Catterall *et al*. 1991; Luck *et al*. 1999; Woinarski *et al*. 2006), while small-bodied native insectivores and nectarivores decline (Barrett 1994; Martin *et al*. 2006). In particular, Martin *et al*. (2006) showed that tree clearing in riparian habitat, resulted in marked changes to bird community composition from a wide range of small-bodied species to a few large-bodied generalist foragers, particularly belonging to the families Corvidae (e.g. Torresian Crow, Australian Raven) and Artamidae (e.g. Australian Magpie, Pied Butcherbird). The same patterns were evident in the brigalow landscape I studied, with fewer functional groups and a higher proportion of large-bodied ground-foraging insectivores in matrix habitats, compared with remnant brigalow.

Many of these large-bodied generalist species have been identified as major contributors to nest predation (Piper and Catterall 2004) and competitive exclusion (Grey *et al*. 1997) and may contribute to the depauperate avian assemblage found in the Brigalow sites. The majority of these generalist species were observed foraging in the matrix adjacent to Brigalow remnants, but still require trees for roosting and nesting. Johnson (2001) noted that many of these granivorous, insectivorous and carnivorous birds use the edge habitat between brigalow forest and the surrounding open pasture and cropland. Matrix habitats surrounding vegetation patches provide these species with supplementary or complementary resources that may not be available in Brigalow remnants (Norton *et al*. 2000; Ries and Sisk 2004).

Among the matrix land management categories in the present study, mean species richness and diversity of birds were greater in uncultivated grassland ($Grass_U$) sites than in previously ($Grass_P$) and currently cultivated (Cultivation) sites. Laiolo (2005) found similar trends, with less intensively managed farmland (e.g. fallow and grassland) supporting a higher diversity of avian species than regularly disturbed maize cultivation. Despite these differences in mean species richness and diversity, multivariate community analyses showed no significant differences in overall bird community composition between any of the matrix land management categories, largely due to high variability of community composition in previously cultivated grasslands and cultivation. This variability may be due to different management practices (Buckingham *et al*. 2006) or the transient nature of bird communities in the matrix as discussed further in Chapter 6.

Studies in Europe have shown that birds respond to changes in land management in the matrix such as conversion from cropping to grassland (Woodhouse *et al*. 2005). However, unlike Australian landscapes, bird assemblages in these European systems are comprised of mostly specialised farmland species. The preference of most Australian bird species for more structurally diverse habitats may mean that in the matrix, they respond to local-scale changes in structural complexity that only occur at later stages of succession such as woody regrowth.

Evidence from other studies suggests that changes in grassland management, such as grazing and weed control, may have significant effects on habitat structural properties such as sward structure and consequently bird communities (Buckingham *et al*. 2006). In the present study, however, there were no differences detected in floristic species richness, patterns of plant community composition (Section 4.3) or habitat complexity of groundcover components (Table 5.5) between the small number of sampled $Grass_U$ and $Grass_P$ sites. Therefore, these local habitat variables can not be used to explain the difference in bird richness and diversity between the two grassland land management categories. Indeed, results from the regression analyses suggest that the richness of matrix bird communities may be affected more by adjacent patch size and landscape composition than by the measured attributes of local-scale habitat complexity.

5.4.3 Habitat and landscape effects on richness, diversity and abundance

Other studies have used a wide variety of patch-scale and landscape-scale metrics to explain the distribution and abundance of organisms in fragmented landscapes (Opdam *et al*. 1984; Mazerolle and Villard 1999). The majority of these studies have focussed on birds, with metrics such as patch size and proportion of suitable habitat commonly used to explain differences in bird species richness and abundance (Loyn 1987; van Dorp and Opdam 1987; Barrett *et al*. 1994). In the present study, regression models suggested that bird species richness in small, fragmented Brigalow remnants surrounded by intensive agriculture, are influenced by a combination of patch-scale habitat variables and landscape context. This finding is similar to those of other recent studies of bird communities in fragmented landscapes (e.g. Sisk *et al*. 1997; Ricketts 2001; Antongiovanni and Metzger 2005; Brotons 2005). In particular, Martin *et al*. (2006) found that 80% of the studied bird species in riparian woodland habitats in southeastern Queensland showed a significant response to both habitat condition and landscape context, while less than 50% of species were influenced by landscape context alone. Furthermore, as surrounding land use became more intensive, the influence of landscape context increased (Martin *et al*. 2006).

In Brigalow remnants, patch-scale (habitat) variables explained a small, but significant amount (17%) of the variance in total bird abundance. This result is consistent with the findings of Mazerolle and Villard (1999), who reviewed 61 studies on the effects of both landscape context and patch characteristics on species presence and abundance in a range of vegetation types. They found that species abundance was significantly explained by patch variables (e.g. area, habitat and shape) in 93% of studies, while the combination of landscape (e.g. habitat area and spatial configuration) and patch variables effectively predicted abundance in 52.5% of studies on vertebrate species. This suggests that both patch and landscape characteristics should be included in studies on the distribution and abundance of vertebrate species.

In the matrix, 56% of the variance in bird species richness was explained by a combination of adjacent patch area and landscape context, with 37% explained by adjacent patch area alone. Despite the measured differences in vegetation floristic composition and structure between matrix land management categories (refer Section 4.3), local habitat variables (e.g. grass and litter cover) were not significant predictors of bird species richness. This finding suggests that the differences in richness and diversity may not be due to local habitat features, but rather, broader characteristics such as adjacent patch size and landscape context or some other variable that was not measured.

5.4.4 Influence of patch size

There is increasing evidence to suggest that small fragmented areas of natural or semi-natural habitat provide important refugia for biodiversity and are thus important for local and regional biodiversity conservation (Fischer and Lindenmayer 2002; Tscharntke *et al.* 2002). Others argue that these small, isolated patches act as population sinks that produce few new individuals to the metapopulation (Donovan *et al.* 1995; Major *et al.* 1999). Despite breeding observations for several bird species that were recorded only in fragmented Brigalow remnants in this study, inferences about whether the small Brigalow patches act as population sources or sinks can not be made. Few large potential ‘source’ patches of brigalow occur in or around the study landscape. Furthermore, the existing small patches are poorly connected by other native vegetation (see Figure 2.4). Although some bird species are able to cross large areas of agricultural land to recolonise the study sites (Brooker *et al.* 1999), other species are limited by their vagility in highly fragmented landscapes and hence may not be able to physically disperse to the isolated study sites (Brooker *et al.* 1999).

However, in the landscape described for my study, 44% of all species were restricted to the few remaining highly fragmented Brigalow patches which comprise around 6% of the cover of the landscape (Chapter 2). Small, degraded remnant Brigalow patches therefore represent a significant and disproportionately large contribution to the avifaunal diversity and conservation value of this landscape. Furthermore, 78% of all species were recorded using vegetation patches, suggesting that the continuing presence of the majority of the bird species in the landscape is influenced by tree or shrub cover of some description. This proportion is similar to the 75% of all species found to occur in small (0.4 – 15.6 ha) patches of woodland in the Nanangroe region of southeastern Australia (Fischer and Lindenmayer 2002). Johnson (2001) proposed that small Brigalow patches may be even more tolerant to fragmentation and able to better support viable bird populations because of their high productivity and resilience (compared with eucalypt woodland), a result of their growth on highly fertile soils.

Contrary to much of the published literature, which shows a positive relationship between patch size and bird species diversity (e.g. Andren 1994; Howe 1984), my results suggest that the richness and diversity of bird communities in small, fragmented Brigalow patches (2-30 ha), are not significantly explained by the size of the patch, but rather by a combination of patch-scale habitat and landscape spatial variables. These findings are similar to those of Watson *et al*. (2000), who concluded that their study sites were too small (<20ha) to display the well documented positive species richness/area relationship. Fischer and Lindenmayer (2002) also detected no significant species-area relationship in small eucalypt remnants in southeastern Australia. In a review of the literature, Bender *et al*. (1998) noted that 'generalist' species, a description that could be used for the majority of bird species recorded in this study, exhibited a negligible response to patch area at a range of spatial scales.

Despite no apparent relationship between patch size and species richness within Brigalow, small remnants are important for predicting bird species richness in the matrix. Regression analyses revealed a strong positive relationship between Brigalow patch area and the species richness of the bird community in the adjacent agricultural matrix. This suggests that bird richness in the matrix may be influenced by the type and extent of adjacent habitat. Similar neighbourhood effects have been noted for other taxa (Dunning *et al*. 1992; Thies and Tscharntke 1999). For example, Dauber and Wolters (2004) showed that ant species diversity in arable land was higher when adjacent to less disturbed habitats such as fallow and meadow areas. However, a comprehensive review of the literature suggests that the relationship between species richness and adjacent remnant area has not been previously documented for bird communities of the matrix.

This observed relationship between avian richness and adjacent patch size may represent an important link between vegetation-dependence in bird species and the provision of ecosystem services in fragmented agricultural landscapes. In particular, many of the species recorded in the matrix are ground-foraging insectivores and may provide beneficial ecosystem services in the form of pest predation in crops and pastures (Tremblay *et al*. 2001; Beecher *et al*. 2002; Sekercioglu 2006). Indeed, studies have shown that many birds act as ‘functional insectivores’ in agro-ecosystems by consuming pest species in crops (Mols and Visser 2002; Jones *et al*. 2005), and that insect pest populations increase when predatory birds are excluded (Tremblay *et al*. 2001). In highly modified landscapes, the abundance of these functional insectivores has been shown to increase with higher landscape heterogeneity (Theis and Tscharntke 1999; Jones *et al*. 2005).

The behaviour of such functional insectivores in agricultural matrix habitats in Australia is little known. Research on those bird species that have been observed foraging on insect pests (e.g. Australian Magpie, Straw-necked Ibis) and how they contribute to agricultural pest suppression, and how they respond to changes in local and landscape-scale agricultural management, is needed to strengthen the evidence of these important functional relationships in fragmented landscapes. The determination of functional roles and thresholds for adjacent patch size for these beneficial species would be of particular use in informing management and ecological restoration efforts. In particular, evidence and clarification of the role of certain species in providing ecosystem services is needed to convince landholders of the tangible benefits of maintaining natural elements in agro-ecosystems.

5.5 Conclusions

Bird community assemblages (as measured by species richness, abundance, diversity, functional group abundance and community composition) were different among land management categories, with richness, abundance and diversity significantly higher and community composition significantly different in Brigalow than in the matrix land management categories.

A combination of habitat complexity of the vegetation and the spatial configuration of the surrounding landscape were shown to influence bird communities in Brigalow remnants. Local-scale habitat factors clearly affect the assemblage of bird species at a particular location in space and time as evidenced by much higher diversity in Brigalow remnants compared with matrix land management categories. However, my research findings support an increasing number of other studies that show that the combination of structure and composition/diversity of the vegetation and the spatial configuration of different components in the surrounding landscape have a significant influence on bird communities in vegetation remnants and in the agricultural matrix (Kupfer *et al*. 2006; Martin *et al*. 2006).

The differences between land management categories emphasise the importance of maintaining small, fragmented Brigalow remnants for biodiversity conservation in agricultural landscapes (Watson *et al*. 2000; Fischer and Lindenmayer 2002). Furthermore, the examination of bird communities across a gradient of agricultural intensification has revealed a number of interesting relationships. For example, the strong relationship between remnant patch area and its effects on bird communities in the adjacent agricultural matrix has not been previously documented. This finding may have important implications for the provision of pest suppression services by birds (Jones *et al*. 2005). This type of information is in great need in agro-ecosystems where the values of native components of the landscape are generally not recognised.

CHAPTER 6

GENERAL DISCUSSION AND CONCLUSIONS

"Despite the significant role of agriculture in altering the Earth's ecosystems, ecologists rarely focus on agriculture" (Robertson 2000, pg 413).

6.1 Overview

Brigalow agro-ecosystems typically evolve along a gradient of increasing land use intensification from remnant vegetation, through secondary and improved grassland to cropland (Altieri 1999). Following long periods of cropping, some areas of cropland may be set aside for natural pasture regeneration, representing a reduction in management intensity. This concluding chapter provides a summary of the major findings from the comparison of ecological indicators in the different land management categories from Chapters 3, 4 and 5. A simple 'state and transition' model (Westoby *et al*. 1989) is used to describe these different land management categories and the transitions between them. Finally, an interpretation of the research is provided in a broader context relating to ecosystem function, resilience and ecosystem services in the studied brigalow landscape, and in agro-ecosystems more generally.

6.2 Changes in agricultural intensification

Historical aerial photographs from the study landscape (1945-2001) show that only small changes in woody vegetation cover have occurred since 1945 (Chapter 2). The majority of land management change during this period has been the conversion of semi-natural grassland (Grass$_U$) to cultivation, with overall grassland cover reducing from 54% to 20% and the cover of cultivation increasing from around 30% to 75% (Figure 2.3).

In its current state, the study landscape consists of natural brigalow vegetation that has been modified to cultivation (cropland) or unimproved (uncultivated) grassland, of predominantly native species. In many cases, conversion to cultivation has been direct – other times indirect through a grassland stage (Figure 6.1). Some cultivated areas have regenerated to form semi-natural grassland communities ('novel ecosystems' *sensu* Hobbs *et al*. 2006) that are similar in diversity and community composition to uncultivated grasslands. In the future, these grasslands may continue to regenerate naturally to later stages of succession such as woody brigalow regrowth. These changes in land management over time can be considered using a 'state and transition' model (Westoby *et al*. 1989;

McIntyre and Lavorel 2007), with the states represented by different land management categories and transitions based on changes in management intensity (Figure 6.1, Table 6.1).

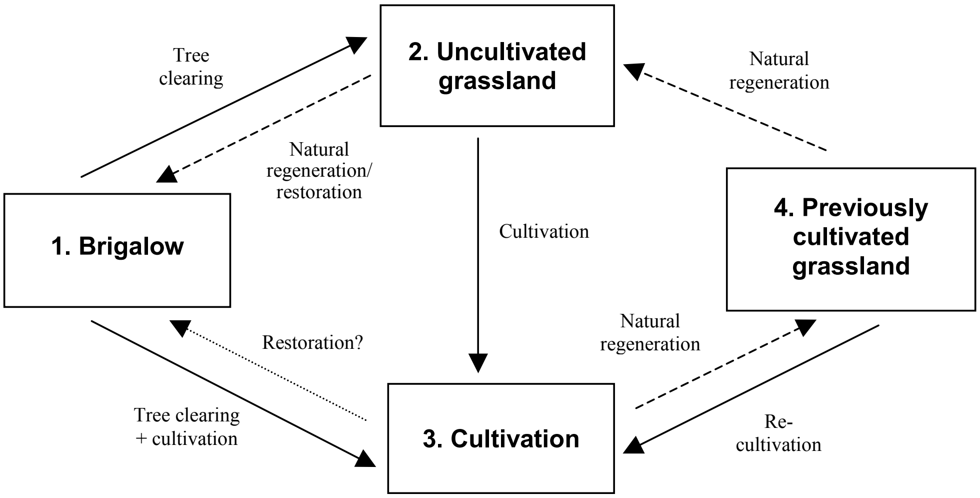

Figure 6.1. Conceptualized pathways ('state and transition model') of agricultural intensification by tree clearing and/or cultivation (solid arrows), potential natural regeneration (dashed arrows), and restoration with human intervention (dotted arrows) between the four land management categories in the study landscape. The four states are described in more detail in Section 2.3.1.

Table 6.1. Transitions between land management categories (states) defined in Figure 6.1, with an indication of the probability of occurring in the present landscape. T_{12} is the transition from State 1 to State 2, T_{21} is the transition from State 2 to State 1, etc.

T_{12}	**Cause**: Clearing of original brigalow vegetation **Probability**: low
T_{23}	**Cause**: Intensification of management from grazing to cropping **Probability**: low-medium
T_{13}	**Cause**: Rapid conversion of brigalow to cropping land **Probability**: low
T_{34}	**Cause**: Land abandonment or extended fallowing for grazing **Probability**: medium
T_{43}	**Cause**: Cultivation of long-term fallows for cropping **Probability**: medium-high
T_{42}	**Cause**: Regeneration of fallow grazing land to semi-natural grassland **Probability**: medium
*T_{21}	**Cause**: Land abandonment with or without human facilitation **Probability**: low
*T_{31}	**Cause**: Restoration by changes to management, soil chemistry and native species plantings **Probability**: low

* potential transitions between land management categories not observed in the study landscape

State and transition models were initially developed to explain multiple successional pathways in rangeland vegetation systems (Westoby *et al*. 1989), but are also applicable to other ecosystem types (Jones and Burrows 1994; Whalley 1994). For example, McIntyre and Lavorel (2007) used a state and transition approach to model plant communities in grassland systems of eastern temperate Australia and Yates and Hobbs (1997a) applied a state and transition model to degraded salmon gum (*Eucalyptus salmonophloia*) woodlands in southwestern Australia. These models provide a useful and flexible framework for developing our understanding of vegetation change (Briske *et al*. 2005) in response to potential shifts in land management such as grazing intensity, cultivation and abandonment. They have been used effectively by scientists to identify gaps in knowledge, focus research questions and communicate the implications of vegetation change (Grice and McIntyre 1995). These models can also be used by landholders to make more informed land management decisions (Whalley 1994) and are useful starting points for ecological restoration (Yates and Hobbs 1997a).

In Australia, state and transition modelling has identified grazing by domestic livestock as the key driver of many vegetation transitions (McIvor and Scanlan 1994; Orr *et al*. 1994). However, in the present brigalow study, more direct human interventions (e.g. land clearing, cultivation) are likely to be the main drivers of transitions between states (Table 6.1). Exceptions are where grazing may affect regeneration/facilitated restoration transitions between grassland and brigalow communities (i.e. T_{34}, T_{42}, T_{21} and T_{31} in Table 6.1).

The majority of Australian studies using a state and transition approach have investigated the effects of disturbance (e.g. grazing, fire) on the herbaceous groundlayer components of grassland and woodland vegetation communities (Orr *et al*. 1994; Grice and McIntyre 1995). However, in the present study, a range of ecological indicators (soil carbon, floristic composition, avian composition) was used to measure differences between land management categories (states) and to gauge the effects of both natural and human-moderated land management changes (transitions) on biodiversity and ecosystem function. This multi-indicator approach may improve the effectiveness of future models for monitoring changes in ecosystem function, particularly in highly modified production landscapes.

6.3 Impacts of agricultural intensification on ecological indicators

The ecological indicators measured in different land management categories along the gradient of intensification displayed distinct trends. However, the nature of these patterns is somewhat indicator-specific. For instance, biodiversity and ecosystem function decreased along the gradient of increasing intensification (i.e. Brigalow > Uncultivated grassland > Cultivation), with some indicators (i.e. plants species richness and cover) increasing in regenerating (Previously cultivated) grasslands. Remnant brigalow patches contributed most to the richness of plant and bird species in the study landscape, despite their small size and high degree of fragmentation (Table 6.2). These remnant areas also contributed to a disproportionately high amount of the overall soil carbon in this landscape (Table 6.2), a finding supported by other studies from Australia (e.g. Dalal and Mayer 1986b; Blair *et al*. 1995) and elsewhere (Murty *et al*. 2002).

Grassland habitats in the agricultural matrix made a lower, yet significant, relative contribution to plant and bird diversity and soil carbon levels, compared with Brigalow. Uncultivated grasslands contained higher soil carbon and greater bird diversity than previously cultivated grasslands; however, plant species richness, percentage cover and community composition were similar between the two grassland land management categories (Table 6.2).

Table 6.2. Summary of differences between land management categories and core and edge sampling locations for the measured indicators of biodiversity and ecosystem function. Reference figures are provided for each indicator. Colours represent differences in the same indicator.

	Brigalow		**Uncultivated grassland**		**Previously cultivated grassland**		**Cultivation**		**Figure reference**
	Core	**Edge**	**Core**	**Edge**	**Core**	**Edge**	**Core**	**Edge**	
Soil Carbon (%)									
Total	a	a	b	b	c	c	c	c	Figure 3.1
Organic	a	a	b	b	c	c	c	c	Figure 3.1
Labile	a	a	b	b	c	c	c	c	Figure 3.1
Plant communities									
Species Richness	a	a	b	b	b	b	c	c	Figure 4.1
%Cover	a	a	b	b	b	b	c	c	Figure 4.2
Composition	a	a	b	b	b	b	c	c	Figure 4.3
Bird communities									
Species Richness	a		b		c		c		Figure 5.1
Diversity	a		b		c		c		Figure 5.1
Abundance	a		b		b		b		Figure 5.1
Composition	a		b		b		b		Figure 5.2

In cultivated areas, levels of soil carbon, bird diversity and plant species richness were lower than in uncultivated grasslands and Brigalow. However, there were no differences in soil carbon concentrations between previously cultivated grasslands and currently cultivated areas (Table 6.2). In contrast to soil carbon, species richness, cover and composition of plant communities were different between currently cultivated and previously cultivated areas; however there were no differences in the plant communities between the two grassland categories. Bird species richness and diversity were lower in currently and previously cultivated areas, compared with uncultivated grassland and Brigalow. However, no differences in abundance and community composition were detected for birds between any of the matrix land management categories (Table 6.2). The significance of these patterns in soil carbon, plant and bird communities will be discussed further in Sections 6.3 and 6.4.

6.3.1 Patterns across edges

Increased plant species richness at habitat edges is commonly reported in ecological studies (Angelstam 1992; Risser 1995). These 'ecotones' often contain higher species diversity than either of the two adjacent habitats because of the composite nature of the species assemblage (Murcia 1995). However, unlike the elevated total plant species richness at remnant edges found in other studies (e.g. Fox *et al.* 1997), the sampled Brigalow remnants in this study had similar total, native and exotic herbaceous plant species richness and community composition at both core and edge (Table 6.2). Grassland and cultivation sites adjacent to the remnants showed similar patterns, with no differences between core and edge within the same land management category. Furthermore, there were no detectable differences in soil carbon levels between core and edge within the same land management category (Table 6.2).

The observed similarity between core and edge for plants or soil carbon in both Brigalow patches and the adjacent matrix suggests that the land use boundaries are abrupt and that adjacent land management categories are discrete in terms of their soil carbon concentrations and plant community assemblages. The relationships at land use edges shown by the data for both soil carbon and plant communities, suggests a step function rather than the hypothesised 'ecotonal' increase at the land use boundary (Figure 6.2). These findings contrast with those of other studies at artificial patch edges (e.g. Fox *et al.* 1997; Ross 2005). In particular, Reis and Sisk (2004) proposed various (empirically-based) theoretical relationships for indicators of ecosystem function at habitat edges. The proposed positive, transitional, and null models were not observed in this study for any of the measured plant or soil carbon variables (Table 6.2, Figure 6.2). The significance of these patterns across edges will be discussed further in Section 6.4.

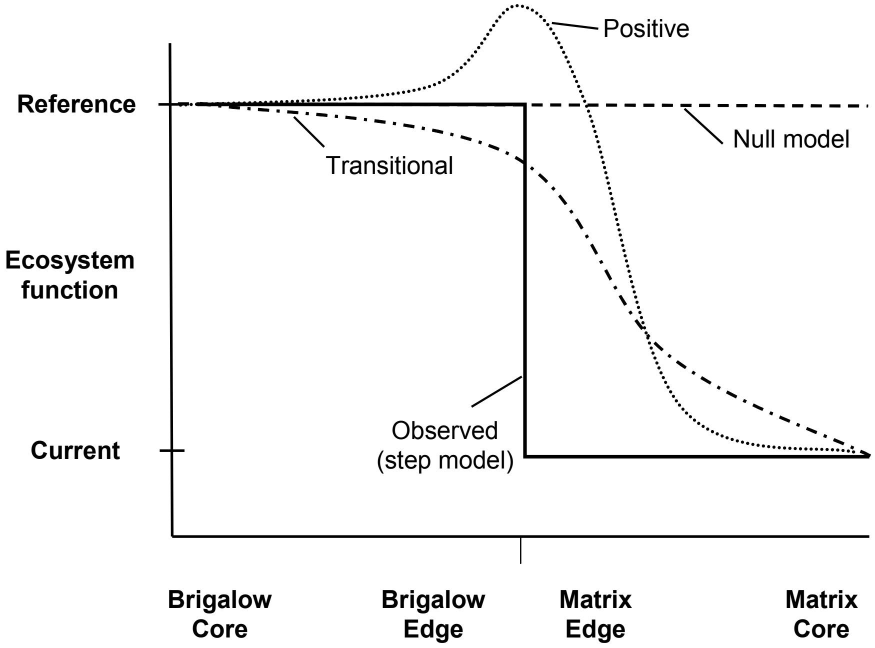

Figure 6.2. Responses of indicators across habitat edges, based on positive, transitional and null models proposed by Ries and Sisk (2004) and the relationship (step model) observed for plant and soil carbon in the present study.

6.4 Comparison of ecological indicators

The selection of appropriate indicators for measuring ecosystem function is critical in ecological studies (Dale and Beyeler 2001; Duelli and Obrist 2003; Perner and Malt 2003). However, the complexities of ecosystems, particularly the trophic and spatial interdependencies between their components, make the selection of representative indicators a real challenge (Walker and Reuter 1996; Dauber *et al*. 2003). Assessing all aspects of biodiversity and ecosystem function within a complex agro-ecosystem is impossible with current assessment techniques. Instead, Freudenberger and Harvey (2003) proposed that biodiversity should be considered as a quantity that cannot be measured in its entirety, but can be regarded as a similarity or difference in measurable characteristics between sites. Hence adequate, measurable correlates or surrogates for ecosystem properties are necessary (Harper and Hawksworth 1994; Duelli 1997), particularly when comparing a range of different land management categories.

The ecological indicators used in this study were chosen to represent a variety of biotic and abiotic factors that reflect land management practices and ecosystem function at a range of trophic and spatial scales. If considered together, these indicators can be effectively used to compare different aspects of biodiversity and ecosystem function between land management categories (Freudenberger and Harvey 2003). The observed differences in the response of indicators to increasing levels of land use intensification and regeneration (Table 6.2) emphasise the importance of using a combination of indicators to detect subtle differences between experimental treatments (Duelli 1997; Andreasen *et al*. 2001; Dale and Beyeler 2001; Duelli and Obrist 2003).

With a few exceptions (i.e. abundance and composition of birds in the matrix), the ecological indicators in the present study showed overall declines along a gradient of increasing agricultural intensification. However, plant communities also showed signs of recovery in previously cultivated grasslands when soil carbon and bird communities did not. These differences can be attributed to responsiveness of different indicators to changes in land management and the scale at which these responses occur. For example, soil carbon concentrations at any particular point in the landscape are largely affected by spatially proximate processes such as plant growth and decomposition (Lucas *et al*. 1977) and therefore change gradually in response to land management practices such as cultivation (Dalal and Mayer 1986b) and grassland regeneration (Reidel and Epstein 2005). In contrast, plants and birds exhibit increased vagility (e.g. seed dispersal for plants and response to resource availability for birds) and can colonise rapidly from elsewhere in the landscape. They are therefore more likely to be affected by broader-scale processes such as landscape composition, configuration and heterogeneity (Benton *et al*. 2003; Bennett *et al*. 2004a). Hence, selected ecological indicators should reflect changes across a range of these spatial and trophic scales.

6.4.1 Landscape context effects

The response of ecological indicators to environmental changes at different spatial scales depends on their behavioural characteristics and trophic level (Sisk *et al*. 1997; Mazerolle and Villard 1999; Ricketts 2001; Brotons *et al*. 2005; Tscharntke *et al*. 2005). In brigalow remnants, a combination of local-scale (habitat) and landscape-scale (context) effects were shown to influence bird species richness. Similar findings have been documented by Bennett *et al*. (2004a), Pearson (1993) and Martin *et al*. (2006) for birds and by Dauber *et al*. (1993) for invertebrates. In the adjacent matrix, local habitat variables were not significant predictors of bird species richness, despite the measured differences in locally-sampled vegetation floristic composition and structure between the different matrix land management categories (refer Section 4.3). This finding suggests that the observed differences in bird richness and diversity in the matrix (Table 6.2) may be due more to landscape factors such as adjacent patch size and landscape context, or some other variable that was not measured, than to the measured local-scale habitat factors.

Plant communities also respond to a combination of factors at different spatial scales. For example, Federoff *et al.* (2005) showed that plant communities reflect land use type and wider land use diversity. However, in the present study, only remnant size and landscape context explained some of the variation in plant species richness in Brigalow patches. Other factors such as soil nutrients and localised management practices affect plant communities (Prober *et al*. 2002*b*); however, in this study these variables were excluded from regression analyses because of the focus on structural and landscape context indicators. In the agricultural matrix, a small amount of the variation in species richness was explained by landscape context variables alone. In contrast, Roschewitz *et al*. (2005) showed that both landscape complexity and local abiotic factors influenced ruderal plant communities in a German agro-ecosystem.

The differences between cultivation and previously cultivated grasslands for plant communities were not apparent for bird communities, despite the higher plant diversity and structural complexity of the regenerating grasslands. The high mobility of birds, particularly the generalist species most commonly recorded in the matrix in this study, is likely to make them less reliable as indicators of local-scale processes (e.g. grassland regeneration) than plants or soil carbon. In particular, many of the bird species recorded in the matrix are transient, readily moving between different land management categories. These species may use certain areas of the matrix to forage for only short periods and therefore may not be detected in short-term monitoring. The value of birds as indicators in these systems lies in their ability to reflect overall landscape-level change.

6.5 Agro-ecosystem function in the context of ecosystem services

The value of native vegetation patches for maintaining biodiversity and ecosystem function in agro-ecosystems is well established (Boulter 2000; Crosthwaite and MacLeod 2000). However, these native areas typically comprise only a small proportion of the overall landscape vegetation cover, with much of the biodiversity occurring outside them (McIntyre and Barrett 1992; Brown *et al*. 2003). Hence, in these production landscapes, there is also growing recognition of the importance of the predominant modified agricultural matrix in providing resilience and a range of ecosystem services beyond food and fibre production (Altieri 1999; Hobbs *et al*. 2006). Intrinsically, these agricultural areas, particularly grasslands, support ‘novel’ and resilient biological communities that benefit rural communities (Altieri 2002; Brown *et al*. 2003).

The broader ecological approach taken in this study enables inferences to be made about both the natural and human-modified (matrix) components of the agricultural landscape. The more traditional ecological approach of focussing on fragmented vegetation patches, which typically comprise only a small proportion of overall landscape cover in agro-ecosystems, and their significance for biodiversity conservation, is complemented by information about the surrounding matrix of grassland and cropland. In highly fragmented agricultural landscapes, this broader 'landscape mosaic' approach (Forman 1995), including measures of ecosystem function in the matrix, provides a better framework for considering overall ecosystem function and ecosystem services in agro-ecosystems (Swift *et al*. 2004).

From this study, a number of inferences can be made about land use intensification and its effects on ecosystem services. These relate to biodiversity conservation, resilience and functional benefits from adjacent land uses and are outlined in more detail below.

6.5.1 Biodiversity conservation and ecosystem function

Results from this study support similar findings in the literature (e.g. Usher 1987; Fischer and Lindenmayer 2002; Gibbons and Boak 2002) that show elevated biodiversity and unique species assemblages in small areas of semi-natural vegetation in agro-ecosystems. Other studies have also identified higher levels of species richness and diversity in the more structurally complex and less intensively managed parts of agricultural landscapes (Arnold *et al*. 1987; Martin *et al*. 2006). For example, 44% of all bird species and 24% of all plant species were found only in Brigalow sampling areas. Many of these species require structurally diverse habitats and therefore do not persist in the surrounding, highly modified and structurally simple agricultural matrix (Arnold *et al*. 1987; Watson *et al*. 2000; Srivastava and Vellend 2005). Large patches of native vegetation are usually of greater significance for biodiversity conservation than small patches in fragmented landscapes. Larger patches are generally able to support viable populations of more species (Major *et al*. 2001; Brown and Sullivan 2005) and are less exposed to pervasive disturbance from the surrounding matrix (Saunders *et al*. 1991; Forman 1995).

However, in some agricultural landscapes, including the one examined in this study, only small, isolated patches of the woody pre-agricultural ecosystems remain. In Queensland, patches of less than five hectares are generally not included in the state-wide government regional ecosystem mapping in Queensland (*Vegetation Management Act 1999*), a spatial dataset that is used for landscape and conservation planning and policy development. The higher species diversity in small Brigalow patches and the presence of rare species such *Grantiella picta* (Painted Honeyeater) and *Homophilis belsonii* suggest that these small remnants are significant for regional biodiversity conservation and should therefore be included in datasets used for landscape planning.

Other, more modified components of the landscape also make a significant contribution to biodiversity and function and the provision of ecosystem services in agro-ecosystems (Altieri 1999; Brown *et al*. 2003). For example, there is increasing recognition that these modified components of agro-ecosystems, including secondary and regenerating grasslands and arable fields, continue to display complex food web interactions and provide a wide array of services that are of uncertain importance for current and future agriculture (Tscharntke *et al*. 2005). Depending on their structural properties and arrangement in space and time, they may also play an important role in facilitating the movement of species between isolated patches of other habitat (Ricketts 2001; Brown *et al*. 2003; Bender and Fahrig 2005; Kupfer *et al*. 2006).

In this study, both secondary and previously cultivated grasslands support significant biodiversity. In contrast, cropping areas are intentionally managed to minimise biodiversity (through weed suppression and cultivation of a monoculture) (Swift *et al*. 2004), and the measured indicators reflected this. However, these intensively managed areas clearly provide ecosystem services through crop production and may contain levels of biodiversity that are functionally viable for their intended purpose (i.e. the production of grain or forage for livestock). Furthermore, these intensively managed areas have been shown to regenerate rapidly in response to less intensive land management practices (Conant *et al*. 2001; Al-Kaisi *et al*. 2005). If embedded in a heterogeneous landscape of mixed land management (e.g. woody vegetation, crops and grassland), these intensively managed systems can benefit from, and provide benefits for overall biodiversity in the landscape (Benton *et al*. 2003).

6.5.2 Agro-ecosystem resilience

The true functional value of some ecosystem components may not be apparent under current conditions and may only be expressed when conditions change (Walker 1995). Yachi and Loreau (1999) referred to this potential response and change in functional importance as the 'insurance hypothesis'. The principle of this hypothesis is that ecosystems with more species have higher stability and are more able to recover from perturbation and species loss than species-poor systems (Holling 1973; Walker 1995). Hence, the lower species diversity in the matrix systems compared with remnant brigalow, may result in the future loss of stability and the ability to recover following change or disturbance (e.g. climate change, weed invasion) (Tscharntke *et al*. 2005; Fischer *et al*. 2006). Furthermore, ongoing species loss in fragmented systems, described by Tilman *et al*. (1994) and Carroll *et al*. (2004) as the 'extinction debt', may further compromise resilience in these landscapes.

In the Brigalow landscape, the ability of grassland plant species to colonise previously cultivated areas reflects the initial stages of succession and potential resilience of these systems. In particular, herbaceous plant cover and overall plant species richness increased following reversion to less intensive management through the cessation of regular cultivation. Indeed, plant species richness and composition in these regenerating grasslands were similar to those in uncultivated grasslands. These ex-arable lands are typically colonised by early successional plant species (Wilcox 1998; Wong 2004). Studies of succession in former agricultural lands ('old-field succession') in other countries have shown that vegetation communities readily move towards a semi-natural state when abandoned (Wilcox 1998; Walker *et al*. 2004; O'Connor 2005), thus restoring plant diversity and rejuvenating natural ecological processes such as nutrient cycling (Parker and Pickett 1997; Knops and Tilman 2000). In contrast, there have been comparatively few published studies on these successional grasslands on ex-arable lands in Australia (*c.f.* Arnold *et al*. 1999; McIntyre and Lavorel 2007) due to the relatively short duration of agriculture in Australian systems.

More than 80% of the land area in the study landscape has been cultivated at some time in the past and 74% is currently under cultivation. If left to regenerate, these cultivated areas provide significant opportunities for colonisation by both native and exotic species (Wong 2004). Research results from this study show that if grasslands are allowed to regenerate naturally following cultivation, perennial native species such as *Dichanthium sericeum* replace these exotic species during an early successional stage, a finding that was also reported by Fensham (1998). These grasslands represent ‘novel’ or ‘emerging’ ecosystems (Hobbs *et al*. 2006) because they result from human intervention and contain a new species assemblage that can potentially cause changes in ecosystem function. Very few previously cultivated areas in the study landscape have been allowed to regenerate for more than 15 years. Consequently, future successional trajectories for these areas are uncertain and would be an interesting topic for further research. Without disturbance, these areas may eventually be recolonised by more structurally complex woody regrowth (Johnson 1964; White and Jentsch 2004) (Figure 6.1).

6.5.3 Interactions between adjacent land uses

In Australian agro-ecosystems, the more structurally complex landscape elements such as native woody remnants generally support more species than the surrounding agricultural matrix (Arnold *et al*. 1987). They also provide a range of benefits for agriculture such as shelter and favourable microclimatic conditions for stock and adjacent crops (Bird *et al*. 1992). Non-crop habitats, interspersed among cropping areas provide a source of beneficial vertebrates (Fowler 1991; Jones *et al*. 2005; Sekercioglu 2006) and invertebrates (Altieri 1999; Tscharntke *et al*. 2002) that may contribute to the suppression of agricultural pests (Tremblay *et al*. 2001) and crop pollination (Blanche *et al*. 2006) by their movement between different land uses. For example, Blanche *et al*. (2006) found that Australian tropical rainforest can act as a reservoir of pollen vectors that benefit adjacent crops. Some disadvantages (dis-services) have also been identified, such as competition with crops for light, moisture and nutrients (Carberry *et al*. 2002).

Lateral movement of biotic material may also occur across edges from one land use to another (Ries and Sisk 2004; van Noordwijk *et al*. 2004). For example, plant seeds and other organic matter pass between land management categories or where animals move between these different habitats to forage (Baudry *et al*. 2000), potentially resulting in a net transfer of organic matter across land use boundaries (van Noordwijk *et al*. 2004). This movement of organic matter between habitats may be important for resilience in these systems and can potentially benefit production in surrounding agricultural areas. Indeed, O'Farrell (2003) found that microbial activity (a measure that is closely linked to labile carbon (Blair *et al*. 1995)) was higher in 'old lands' adjacent to Renosterveld vegetation edges in South Africa, and reduced with distance away from the native vegetation edge. Similarly, Riedel and Epstein (2005) observed a more advanced stage of plant succession in old-fields adjacent to secondary forest in Virginia.

In contrast to these findings of enhanced biological activity in agricultural areas near vegetation edges, this study found that soil carbon concentrations and herbaceous plant community richness, abundance and composition were similar at core and edge in the matrix adjacent to remnant brigalow. These defined boundary effects and the observed homogeneity within land uses might be expected for soil attributes, which are more likely to respond to local, rather than landscape-scale management changes (Lucas *et al*. 1997). For example, regeneration of soil carbon is typically a slow process in previously cultivated lands because it results largely from locally-derived biomass turnover and decomposition (Knops and Tilman 2000). The slow recovery of soil carbon has been documented by Riedel and Epstein (2005) who found no significant increase in soil carbon levels in old-fields that were in close proximity to secondary forest in Virginia after 14 years. Furthermore, Knops and Tilman (2000) estimated that it would take 230 years for soil carbon to return to pre-agricultural levels following abandonment of agricultural fields in Minnesota. In this study, any net movement of organic matter from remnant patches into the adjacent matrix, particularly in cultivated areas, would probably be negated by frequent disturbances caused by agricultural management practices such as tillage, herbicide and fertiliser application.

In the brigalow landscape, the similarities between core and edge in the same land management category for soil carbon were also observed for plant communities, which are expected to exhibit high seed dispersal and rapidly colonise surrounding areas (Devlaeminck *et al*. 2005). In particular, differences in plant communities might have been expected between the core and edge of previously cultivated grasslands if remnant patches were providing a source of seeds to adjacent fields (Riedel and Epstein 2005). However, the absence of any detectable difference may suggest that the propagules of the plant species colonising these previously cultivated areas are sourced from the matrix components of the surrounding landscape and not from the adjacent Brigalow remnant. Indeed, Devlaeminck *et al*. (2005) found that the most abundant species in the seed bank in a field adjacent to deciduous forest in Belgium did not originate from the nearby forest. Alternatively, some other environmental factors such as seed predation (Bustamante *et al*. 2003) or sensitivity to sunlight exposure (Scanlan 1991; Murcia 1995) may have affected the germination and establishment of seeds from Brigalow remnants.

The absence of any detectable edge effects for plant communities and soil carbon within brigalow patches may be due to the small size and high disturbance of the remnant patches. Compared with larger remnant patches, small patches may be more susceptible to the effects of disturbance from grazing, spray drift, fire, exotic species invasions or increased light intensity (Murcia 1995), potentially leading to the observed homogeneity in plant communities and soil carbon levels within small patches. In the present study, the sampled patches may not have been large enough to contain a core area that was buffered against the effects of modification and fragmentation in the surrounding landscape (Forman 1995). An alternative hypothesis, that these patches are resilient to edge effects, is unlikely given the recorded presence of exotic plant species and similar frequency and intensity of grazing at the core and edge of Brigalow remnants, suggesting some degree of pervasive disturbance.

Spatial analyses partially contradict these local-scale edge findings. In particular, brigalow patch size strongly influenced bird species richness in the adjacent agricultural matrix, with increased species richness and diversity of birds adjacent to larger brigalow patches. This suggests some interaction between land management categories such as the movement of bird species from remnants into the adjacent agricultural matrix. However, bird communities were not sampled at core and edge in the present study because of the potential for overlapping sampling areas in small patches. Unlike plants and soil, their high mobility may mean that they are less affected by local management practices in the matrix.

The most common bird species in the matrix were ground-foraging insectivores that potentially regulate insect populations in these areas. Jones *et al*. (2005) described such species as 'functional insectivores' because of their contribution to pest control and potential benefits for production (Tremblay *et al*. 2001; Sekercioglu 2006). The movement of these species across habitat edges was observed in the field and most of these generalist species require the trees in adjacent remnants to nest and roost. However, in order to establish the functional value of these bird species in agro-ecosystems, further research is needed on their abundance, movement patterns across land use edges and foraging behaviour.

6.6 Implications for management

It is clear that existing native remnant vegetation supports higher species diversity than matrix land uses and should therefore be protected and maintained for conservation. For example, approximately 44% of all bird species and 24% of all plant species recorded in this study are obligate forest/woodland species that did not occur outside the remaining fragmented forest patches in the landscape during the sampling period. Hence, these brigalow remnants, which comprise less that 6% of overall landscape cover, should be maintained for their intrinsic biodiversity value as well as for the benefits they provide to current and future production activities. Significant opportunities also exist for enhancing biodiversity and ecosystem function in the study landscape, particularly in cultivated areas, as shown in the state and transition model (Figure 6.1). Regenerating grassland assemblages in ex-arable areas were similar in species richness and community composition to uncultivated secondary grasslands after short regeneration times (3-15 yrs). Potential mechanisms for this transition to semi-natural grassland and later successional stages are shown in Figure 6.3.

Increasing intensification from remnant vegetation to uncultivated grassland to cultivation leads to a decline in ecosystem function. This intensification gradient and its effects on ecosystem function is shown in Figure 6.3. Future options for managing ecosystem function in the study landscape are proposed as a result of this research (Figure 6.3). These include: a) continuing with current cropping practices with limited or no inputs (additional to current levels of crop residue incorporation), leading to potential further declines or maintenance of ecosystem function at the current low levels; b) natural grassland regeneration, leading to a potential increase in ecosystem function and resilience over time; and c) natural establishment of woody vegetation following an initial grassland regeneration stage, leading to increases in function in the landscape, generally over longer time periods (Figure 6.3).

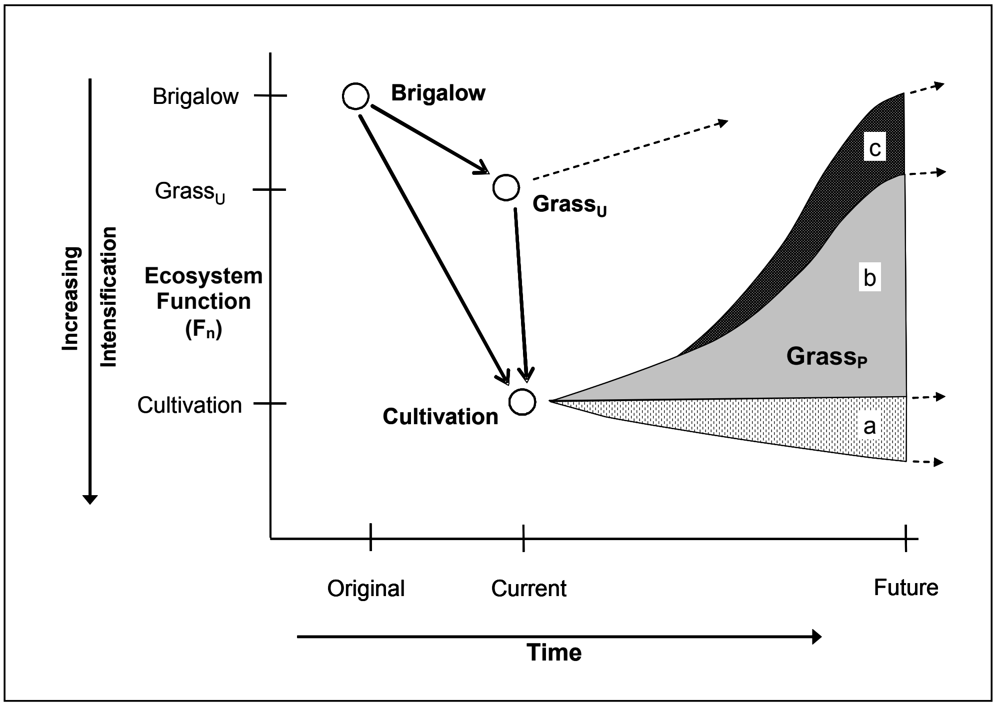

Figure 6.3. Land management categories represented along a gradient of intensification and ecosystem function (F_n) showing potential future options and pathways of regeneration including a) status quo, b) regenerating grassland c) regenerating woody Brigalow vegetation.

Observed patterns in the study landscape suggest that soil carbon in cultivated areas may continue to decline or remain at measured levels if current practice continues (trajectory ‘a’ Figure 6.3). However, if allowed to regenerate for longer periods, soil carbon concentrations would be expected to follow trajectory ‘b’, as biological activity and turnover increase, eventually leading to soil carbon replenishment (Knops and Tilman 2000; Conant *et al*. 2001; San Jose *et al*. 2003). Plant communities, which regenerated in the study landscape after cultivation ceased, would fall somewhere within trajectory ‘b’ and could potentially develop into more structurally diverse woody vegetation in a later stage of succession (i.e. trajectory ‘c’). Bird community richness and abundance would be expected to increase as the structural complexity of the vegetation increased in later successional stages. Furthermore, this and other studies have shown that plant and bird communities are also strongly influenced by management changes at broader landscape and regional scales (Bennett and Ford 1997; Federoff *et al*. 2005).

6.7 Study limitations

Investigations in other agricultural landscapes, with an increased number of available sampling sites in the grassland land management categories (i.e. a more balanced design), would strengthen these research findings and our understanding of the response of soil carbon and plant and bird communities to changes in land use intensity. In particular, the absence of any detectable increase in soil carbon levels in regenerating grasslands, compared with currently cultivated areas is contrary to the majority of the reviewed literature on this topic. Therefore, my results require substantiation with a greater number of study sites, ideally with less variation in management practices such as time since cultivation. Time since cultivation is an important determinant of soil carbon recovery in ex-arable lands (Knops and Tilman 2000), and of recruitment and successional patterns in plant communities (Pickett 1982). An increased number of grassland sites would also enable comparisons to be made at boundaries between matrix land management categories e.g. Grass_{P}/Grass_{U}, Grass_{U}/Cult and Grass_{P}/Cultivation. However, despite these limitations, a number of strong trends, consistent patterns and new findings have emerged in relation to land use intensification and its effects on biodiversity and ecosystem function. These findings provide a strong basis for further ecological research in these systems.

Categorisation and interpretation of the spatial data for landscape analyses was constrained by the ability to differentiate between land management categories using the available aerial photography. For example, only three broad land management categories (Brigalow, Grassland and Cultivation) were used to spatially classify the study landscape as it was not possible to separate uncultivated and previously cultivated grasslands. Further division and spatial mapping of grassland and cropping types based on spatio-temporal variation in management regimes in the matrix (e.g. grazing, tillage practices, crop rotations) would therefore provide additional information and allow stronger inference about the impact of land management on ecosystem function across the landscape. Spectral imaging could be used in this context to differentiate more accurately between land uses (Wessman 1991).

This study examined differences between land management categories and the effects of landscape context on ecological function. Although this approach has been appropriate for addressing the research questions, agro-ecosystems typically exhibit high temporal variability such as seasonal and annual changes in management and biological communities, particularly in the agricultural matrix. These changes may have a significant impact on biodiversity, ecosystem function and resilience in these systems and therefore should be considered in more detail in future studies. As noted earlier, there has also been a prolonged period of below average rainfall in the study landscape; ecological surveys during a wetter climatic cycle would further strengthen the current dataset and may provide additional information on the effects of agricultural intensification on ecosystem function, particularly in relation to soil carbon recovery.

6.8 Conclusions

The research presented in this dissertation makes a significant contribution to the existing knowledge and understanding of the role of remnant brigalow, grassland and cultivated areas in maintaining biodiversity and ecosystem function in the study landscape, and in agro-ecosystems more generally. Prior to this study, ecological research in brigalow landscapes has been largely restricted to the characterisation of larger vegetation patches and spatial mapping of remnant brigalow communities. This research highlights the value of small patches of these vegetation systems and the importance of the surrounding landscape for maintaining biodiversity and ecosystem function.

The key research findings from this study are:

- Land management categories along a gradient of agricultural intensification contributed in different ways to biodiversity and landscape-scale ecosystem function. Remnant brigalow vegetation contained significantly higher soil carbon, species richness and diversity and was compositionally different from other matrix land management categories. The grassland components of the landscape also made a significant contribution. Predictably, intensive cropping areas contributed little to overall biodiversity and ecosystem function. However, these cultivated areas showed signs of resilience following the cessation of regular tillage.

- There was no detectable gradient in soil carbon or plant community diversity or composition within land management categories. In particular there were no detectable differences in soil carbon and plant communities between the core and edge of any of the land management categories. This finding in remnant vegetation is contrary to much of the literature and may be caused by the small size and highly fragmented nature of the remnant patches.

- Spatial variables such as remnant patch area and landscape context (the composition and configuration of the surrounding landscape) had a greater effect on locally sampled plant and bird communities in both Brigalow and the matrix than the measured structural variables.

This research has provided some useful insights into measuring biodiversity and ecosystem function in brigalow agro-ecosystems. For example, while most previous ecological studies in agricultural landscapes concentrate on vegetation remnants (Robertson 2000) this study highlights the advantages of using a broader approach, one that encompasses both the natural and modified components of the landscape.

Measured indicators showed overall declines along a gradient of agricultural intensification. However, despite the decreasing trend overall, some more subtle patterns and differences were evident in the matrix. As previously noted, different indicators of biodiversity and function responded in different ways to changes in land management in heterogeneous agro-ecosystems. This variability emphasises the importance of selecting a range of ecological indicators that reflect land management changes at both local and broader spatial scales. When considered together, the indicators used in this study were useful in comparing different aspects of biodiversity and ecosystem function between and within land management categories.

Furthermore, some useful inferences can be made about ecosystem services, based on these results. The higher native biodiversity in small remnant brigalow patches, compared with the matrix, emphasises the importance of these areas for local and regional biodiversity conservation and ecosystem services at wider spatial scales. In addition, some of the findings provide useful information for considering ecosystem services at finer scales. For example, biodiversity and ecosystem function were significantly lower in intensively managed (cultivated) parts of the landscape compared with the less intensively managed (uncultivated) grassland and vegetation components. In particular, the lower soil carbon in these intensively managed areas can affect agricultural production activities by affecting ecosystem services. The positive relationship between brigalow patch size and bird species richness in the adjacent matrix also provides evidence of a potential increase in ecosystem services associated with remnant vegetation.

The research presented in this dissertation has provided information that is of direct relevance to land managers in highly modified and fragmented brigalow landscapes and in agro-ecosystems more generally. The most important of these findings is that in order to maintain biodiversity and ecosystem function, small remnant vegetation patches should be retained and complemented by less intensive management of novel ecosystems in the agricultural matrix such as grasslands.

6.9 Management recommendations and future directions

On the basis of this study, a number of recommendations can be made about land management practices that can potentially enhance biodiversity and ecosystem function in the study landscape:

- **Maintain existing brigalow remnants**

Small patches of remnant woody vegetation play a valuable role in maintaining native biodiversity in agro-ecosystems. In some landscapes, particularly agro-ecosystems, protection and restoration of small patches is the only feasible management option (Fischer and Lindenmayer 2002). In the southern Brigalow Belt, Johnson (2001) highlighted the urgent need to recognise the conservation value of these small brigalow remnants on private land for them to be maintained. Where native vegetation cover falls below a critical level, greater importance should be placed on protecting and maintaining small remnants. These small remnants should also be given higher priority in local and regional biodiversity conservation planning. The small remnant patches in this study, while contributing significantly to overall biodiversity and ecosystem function are currently not protected by legislation.

- **Recognise the intrinsic value of the matrix for biodiversity and ecosystem services – protect and maintain 'novel ecosystems'**

Currently in the study landscape, remnant brigalow vegetation comprises only 6% of overall landscape cover. Therefore, a significant component of the overall biodiversity in the landscape is contained in the other 10% of grassland areas (including uncultivated and previously cultivated grasslands) and cropping lands (84%). Preservation and enhancement of the grassland areas, combined with regeneration in ex-arable lands can potentially enhance local and landscape-scale biodiversity values and ecosystem productivity. The grassland components in particular are likely to provide a different range of functions and services compared with Brigalow and cultivated areas and these grassland areas should therefore be retained and managed.

Most ecological studies and legislative models for biodiversity conservation are still focussed on patches of native vegetation (Kupfer *et al*. 2006). However, there is a trend towards ecological research in areas outside designated conservation reserves into the modified matrix components of agricultural landscapes (McIntyre and Barrett 1992; Hobbs *et al*. 2006) or at least considering the effects of the matrix on remnants (Kupfer *et al*. 2006). In the Brigalow Belt bioregion this approach is particularly vital, considering the very low native vegetation cover in some areas (Sattler and Williams 1999).

- **Where possible, provide opportunities for improved management and natural regeneration in the matrix.**

The natural regeneration of plant communities in previously cultivated areas to novel grassland assemblages with species richness and community composition resembling uncultivated grasslands, suggests that these areas may be important for maintaining and restoring overall biodiversity, resilience and ecosystem function. Management and restoration efforts should consider not only local-scale habitat features, but also the spatial composition and configuration of the surrounding landscape (Ricketts 2001).

In the case of soil carbon in cropping areas, sustainable crop management practices such as minimum tillage and manure application of carbon inputs can potentially be used to raise carbon levels above current levels (Karlen and Cambardella, 1996; Solomon *et al*. 2000). Such management practices would in turn improve soil fertility, soil structure and soil water-holding capacity (Matson e*t al*. 1997), providing functions that are important for ecosystem regulation and the provision of ecosystem goods and services to humans (Daily *et al*. 1997).

6.9.1 Future research opportunities

- **Examine different ecological and socio-economic indicators in this and other landscapes**

This study has emphasised the importance of using a ‘multi-indicator’ approach for reflecting different aspects of ecosystem function in agro-ecosystems (Andreason *et al*. 2001; Bouma 2002). A broader range of ecological indicators and their functional groups may detect other more subtle differences between land management categories (Swift *et al*. 2004). For example, Perner and Malt (2003) suggest that beetles and ground-dwelling spiders may be more responsive to changes in management than plant communities and should therefore be used for monitoring of short-term restoration projects. Other studies show that invertebrates are linked to both local habitat modification and to changes in landscape context (Dauber *et al*. 2003). Furthermore this set of indicators should ideally be examined in landscapes with different levels of landscape modification and fragmentation.

In Australia, the biodiversity component of the national ‘Grain and Graze’ project is investigating invertebrates in a range of different natural and modified landscape components in mixed farming systems across Australia (Land and Water Australia 2006, accessed 20/12/2006). This national project is also investigating a range of socio-economic indicators in mixed farming systems. Although these aspects were briefly examined in the early stages of this dissertation, further analysis of ecosystem services will require comprehensive and explicit consideration of social and economic issues.

- **Investigate link between remnant size and bird species richness**

The observed relationship between avian richness and adjacent patch size may represent an important link between vegetation-dependence in bird species and the provision of ecosystem services (e.g. agricultural pest suppression) in fragmented agricultural landscapes. Further investigation on the types and behavioural attributes of bird communities adjacent to vegetation patches may provide important information on the functional role of some of these species and their contribution to pest suppression. More specifically, further investigation is warranted on the hypothesis that as patches increase in area, species richness in the adjacent matrix also increases.

- **Investigate subtleties in land management in the matrix**

In this study, areas of the matrix were broadly assigned to land management categories (or states) according to grassland type and time since cultivation (Figure 6.1). Despite these land management categories having similar structural attributes, subtle differences in land management practices by individual land holders may also affect measured indicators within these groups. For example, changes in land management such as type and rotation of crops, frequency and amount of fertiliser and herbicides applied, time since cultivation and grazing intensity may influence measured ecological indicators. Accounts from land managers at the time of sampling suggested that management practices in similar land management categories were essentially the same, however, more detailed information may be valuable in explaining some of the more subtle variations in measured indicators.

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Appendix 1. Spatial variables used in multiple linear stepwise regressions in Chapters 4 and 5.

Table A1.1. Spatial variables, derived using aerial photographs and GIS, including area in hectares (Area), number of patches (NumP) and mean patch size (MPS) for Brigalow, Grassland and Cultivation land management categories within 500, 1000, 1500 and 2000 m buffer areas around study sites.

Study site number	Area 500	Area 1000	Area 1500	Area 2000	NumP 500	NumP 1000	NumP 1500	NumP 2000	MPS 500	MPS 1000	MPS 1500	MPS 2000
Brigalow												
1	41.2	63.0	74.8	135.0	4	13	30	63	10.0	4.7	2.8	2.2
2	20.6	59.5	74.0	134.2	3	10	29	48	6.6	5.8	2.5	2.7
3	11.6	23.6	41.7	94.0	6	18	39	53	1.6	1.1	1.0	1.7
4	13.6	25.3	36.6	78.1	8	22	35	61	1.4	1.0	0.9	1.2
5	6.6	46.2	87.7	109.5	3	11	17	34	2.0	4.1	5.0	3.1
6	6.5	24.1	79.3	117.5	3	8	18	37	1.8	2.8	4.2	3.1
7	13.8	31.1	71.1	112.8	6	14	24	32	2.3	2.2	2.9	3.4
8	16.2	28.3	46.2	87.9	5	15	24	39	3.2	1.8	1.8	2.2
9	7.6	16.7	36.7	81.1	7	11	18	30	1.1	1.5	2.0	2.6
10	11.8	20.9	38.5	79.0	9	13	23	40	1.4	1.6	1.5	1.9
11	6.8	21.6	34.4	50.7	4	10	19	33	1.5	2.0	1.7	1.4
12	6.3	19.6	58.2	96.1	5	11	24	53	1.2	1.6	2.3	1.7
13	5.0	25.7	41.1	84.4	4	15	29	52	1.3	1.6	1.3	1.5
14	13.1	35.4	70.0	96.9	11	29	40	55	1.2	1.2	1.7	1.7
15	9.4	25.5	53.0	80.8	7	17	44	59	1.6	1.6	1.2	1.4
16	2.1	33.9	67.8	113.4	11	22	39	54	1.1	1.5	1.7	2.1
17	9.2	11.9	30.2	48.2	1	3	10	19	8.8	3.8	2.9	2.5
18	7.9	13.0	41.1	61.9	1	9	15	33	8.4	1.4	2.6	1.8
19	5.9	19.3	62.5	79.8	2	8	19	25	3.3	2.4	3.3	3.1
20	5.3	15.3	30.6	76.0	1	7	15	32	6.0	2.2	2.0	2.3

Study site number	Area 500	Area 1000	Area 1500	Area 2000	NumP 500	NumP 1000	NumP 1500	NumP 2000	MPS 500	MPS 1000	MPS 1500	MPS 2000
Grassland												
1	58.6	103.9	205.6	350.9	23	43	81	113	1.1	1.7	2.0	2.8
2	19.3	46.5	121.4	237.2	20	43	58	94	0.6	0.9	2.0	2.5
3	30.7	94.9	172.5	271.8	5	24	74	109	5.8	3.9	2.3	3.0
4	33.4	85.0	177.1	261.4	8	38	73	117	3.7	2.2	2.4	2.2
5	9.2	42.5	90.5	185.3	5	31	65	96	1.3	1.3	1.4	1.9
6	20.5	45.9	106.2	238.4	5	22	63	83	3.4	2.0	1.7	2.9
7	24.9	64.6	136.9	251.2	8	26	60	79	2.7	2.4	2.3	3.2
8	14.2	61.2	170.7	288.9	18	38	38	71	0.7	1.6	4.5	4.1
9	63.8	95.3	162.4	212.0	2	13	27	72	30.9	7.2	6.0	3.0
10	56.4	125.4	193.2	275.1	12	16	38	62	4.3	7.6	5.1	4.4
11	24.9	67.8	173.9	235.0	9	29	34	39	2.6	2.3	5.1	6.1
12	29.0	117.3	209.0	276.9	4	7	30	95	6.8	16.7	7.0	3.0
13	38.5	110.1	228.4	291.4	5	18	38	101	7.2	6.1	6.0	2.9
14	46.7	95.8	172.7	273.7	10	26	71	118	4.7	3.7	2.5	2.3
15	15.5	54.3	164.0	247.1	25	51	71	83	0.5	1.0	2.3	3.0
16	37.8	73.0	149.4	244.3	8	40	57	126	3.7	1.8	2.6	1.9
17	38.7	83.8	156.9	299.8	3	9	17	38	10.1	8.4	8.8	7.7
18	22.9	80.2	186.3	327.1	6	23	33	46	2.5	3.2	5.5	7.0
19	17.4	70.4	195.9	383.7	7	13	40	47	2.1	5.2	4.9	8.2
20	6.3	59.4	133.1	274.3	12	18	30	48	0.2	3.2	4.4	5.7

Study site number	Area 500	Area 1000	Area 1500	Area 2000	NumP 500	NumP 1000	NumP 1500	NumP 2000	MPS 500	MPS 1000	MPS 1500	MPS 2000
Cultivation												
1	204.5	490.1	882.6	1337.0	2	5	11	24	85.5	91.3	77.2	54.3
2	124.8	350.0	705.7	1128.8	3	8	10	17	38.8	42.7	69.7	65.9
3	81.1	271.2	596.2	1020.4	4	8	15	18	19.4	33.4	39.5	53.7
4	94.4	309.7	639.6	1101.7	3	9	14	15	29.6	33.8	45.3	73.1
5	100.0	288.8	610.9	1069.6	3	4	6	17	32.4	71.5	101.7	62.8
6	98.7	322.9	628.6	1033.7	3	6	10	13	31.6	53.2	62.5	79.2
7	96.3	315.5	632.9	1060.3	4	5	8	13	23.1	62.3	78.6	81.3
8	87.9	293.1	584.2	997.7	2	10	15	16	42.6	29.0	38.8	62.2
9	40.9	260.3	587.3	1061.7	5	10	10	6	7.8	25.8	58.5	176.6
10	71.7	273.2	621.5	1086.6	6	9	10	9	11.2	29.9	61.7	120.2
11	80.7	282.6	577.7	1068.5	3	5	9	12	26.2	56.1	63.9	88.9
12	79.2	239.1	524.6	989.1	3	7	11	15	25.7	33.8	47.5	65.8
13	77.9	252.9	541.1	1011.1	4	8	10	16	18.8	31.3	53.8	63.0
14	55.8	251.0	560.1	1006.8	6	10	12	14	9.3	25.1	46.7	71.9
15	110.5	335.5	632.4	1109.8	7	4	11	16	15.4	83.2	57.2	69.2
16	77.2	264.9	569.1	998.2	2	4	11	10	33.4	65.8	51.6	99.6
17	115.9	359.4	713.1	1151.6	2	10	11	16	53.7	35.1	64.1	71.5
18	124.5	348.0	653.7	1086.8	2	6	13	11	58.4	56.7	49.7	98.1
19	102.8	307.4	564.0	938.5	3	6	12	12	33.3	50.8	46.8	78.0
20	133.7	357.2	708.9	1117.3	1	5	6	12	129.8	70.6	117.5	92.8

Appendix 2. Raw total, organic and labile soil carbon data at Brigalow Core, Brigalow Edge, Matrix Core and Matrix Edge

Table A2.1. Total (%), organic (%) and labile (mg/kg) soil carbon concentrations at core and edge sampling locations at 22 study sites.

	Brigalow Core			Brigalow Edge			Matrix Edge			Matrix Core		
Site #	**Total**	**Organic**	**Labile**	**Total**	**Organic**	**Labile**	**Total**	**Organic**	**Labile**	**Total**	**Organic**	**Labile**
1	6.36	6.27	16.90	5.86	5.70	15.23	2.83	2.53	5.47	1.94	1.70	3.97
2	4.39	3.87	10.38	8.09	6.81	20.43	1.73	1.12	2.32	2.33	1.66	3.65
3	6.44	4.90	13.50	7.45	6.48	17.74	5.27	4.60	11.19	5.09	4.60	11.90
4	5.09	4.81	13.59	6.18	5.15	16.69	2.04	1.35	3.41	1.67	1.25	3.25
5	7.11	6.19	17.84	8.48	6.76	20.45	2.02	1.35	2.76	1.58	1.16	2.85
6	6.67	5.99	16.05	5.33	4.79	12.49	2.98	2.39	4.65	2.65	2.39	3.88
7	6.25	6.28	17.10	6.90	5.35	13.97	2.21	1.55	3.40	2.44	1.85	3.62
8	6.61	6.43	19.12	4.50	4.27	10.83	4.82	4.02	9.88	2.55	2.02	4.07
9	6.90	5.52	14.95	6.45	6.00	18.32	1.82	1.23	2.39	1.81	1.12	2.16
10	4.24	3.48	9.69	5.91	4.58	13.99	1.63	1.20	2.53	1.82	1.39	2.92
11	6.27	6.10	16.78	4.11	3.38	8.47	3.21	2.45	5.10	2.37	1.65	3.14
12	7.77	6.48	19.14	6.28	5.56	16.39	4.39	3.95	9.94	3.83	3.56	8.63
13	5.34	4.27	12.24	5.77	5.49	15.00	1.60	1.18	2.19	1.90	1.49	3.72
14	6.08	4.95	13.46	5.47	4.68	11.62	2.28	1.62	3.74	3.17	2.77	6.20
15	7.64	6.93	18.34	6.32	5.64	15.03	2.46	2.09	4.25	2.16	2.18	4.31
16	3.80	3.09	8.06	3.72	3.12	8.00	1.93	1.41	3.65	1.37	0.95	2.08
17	6.13	5.91	16.39	7.04	5.73	16.41	4.23	4.49	9.39	3.78	3.86	8.64
18	4.52	4.70	9.49	8.19	6.91	18.85	2.82	2.49	4.47	1.66	1.26	1.79
19	5.54	4.83	13.22	4.65	4.61	12.38	1.46	1.26	3.44	0.71	0.45	1.31
20	4.97	4.87	12.37	4.18	4.01	9.49	2.07	1.79	5.12	2.16	1.52	4.05
21	6.76	5.45	15.56	4.92	4.18	11.38	1.43	1.05	2.16	1.51	0.98	1.90
22	5.28	4.84	13.62	9.22	8.29	23.97	2.27	1.87	3.63	2.51	2.08	4.05

Appendix 3. Pearson correlation matrix for spatial variables (Table A3.1) and habitat variables (Table A3.2) used for regression and analyses in Chapters 4 & 5. * Correlation is significant at the 0.05 level (2-tailed). ** Correlation is significant at the 0.01 level (2-tailed).

Table A3.1. Correlation table for landscape context variables used in regression analyses in Chapters 4 and 5. Column and row labels are described in Appendix 1. Matrix continued overleaf.

	Veg500	**Veg1000**	**Veg1500**	**Veg2000**	**Graz500**	**Graz1000**	**Graz1500**	**Graz2000**	**Cult500**	**Cult1000**	**Cult1500**	**Cult2000**	**PatchArea**	**NPVeg500**	**MPSVeg500**	**NPVeg1000**	**MPSVeg1000**	**NPVeg1500**	**MPSVeg1500**
Veg500	1.00																		
Veg1000	0.72**	1.00																	
Veg1500	0.40	0.75**	1.00																
Veg2000	0.59**	0.82**	0.83**	1.00															
Graz500	0.25	-0.07	-0.10	-0.04	1.00														
Graz1000	0.07	-0.23	-0.23	-0.17	0.80**	1.00													
Graz1500	0.03	-0.27	-0.30	-0.32	0.54*	0.83**	1.00												
Graz2000	-0.25	-0.46*	-0.23	-0.35	0.01	0.35	0.64**	1.00											
Cult500	-0.46*	-0.10	0.01	-0.10	-0.97**	-0.74**	-0.50*	0.05	1.00										
Cult1000	-0.39	-0.24	-0.13	-0.21	-0.76**	-0.88**	-0.67**	-0.11	0.78**	1.00									
Cult1500	-0.24	-0.16	-0.28	-0.14	-0.49*	-0.71**	-0.83**	-0.50*	0.49*	0.76**	1.00								
Cult2000	-0.08	-0.02	-0.28	-0.24	0.03	-0.24	-0.44*	-0.83**	-0.01	0.22	0.59**	1.00							
PatchArea	-0.30	-0.29	-0.44	-0.27	-0.38	-0.41	-0.32	0.05	0.41	0.53*	0.59**	0.10	1.00						
NPVeg500	0.73**	0.41	0.24	0.35	0.63**	0.47*	0.28	-0.17	-0.74**	-0.63**	-0.40	-0.01	-0.35	1.00					
MPSVeg500	-0.50*	-0.42	-0.44*	-0.40	-0.47*	-0.46*	-0.35	0.15	0.53*	0.62**	0.62**	0.07	0.84**	-0.63**	1.00				
NPVeg1000	0.68**	0.49*	0.27	0.37	0.38	0.32	0.27	-0.05	-0.49*	-0.51*	-0.41	-0.14	-0.25	0.86**	-0.50*	1.00			
MPSVeg1000	-0.11	0.27	0.15	0.18	-0.47*	-0.66**	-0.67**	-0.33	0.44*	0.481*	0.58**	0.21	0.55*	-0.49*	0.61**	-0.47*	1.00		
NPVeg1500	0.64**	0.49*	0.22	0.40	0.19	0.15	0.21	-0.07	-0.31	-0.35	-0.31	-0.14	-0.04	0.72**	-0.38	0.86**	-0.28	1.00	
MPSVeg1500	-0.35	0.13	0.51*	0.25	-0.41	-0.54*	-0.63**	-0.19	0.45*	0.44	0.31	0.00	0.10	-0.52*	0.27	-0.53*	0.60**	-0.58**	1.00
NPVeg2000	0.45*	0.43	0.11	0.37	0.11	0.16	0.19	-0.13	-0.18	-0.33	-0.24	-0.06	0.15	0.56*	-0.20	0.72**	-0.14	0.87**	-0.49*
MPSVeg2000	-0.06	0.17	0.47*	0.39	-0.27	-0.48*	-0.60**	-0.12	0.26	0.38	0.34	-0.14	0.04	-0.36	0.18	-0.46*	0.52*	-0.50*	0.80**
NPGraz500	0.35	0.29	-0.05	0.10	-0.42	-0.47*	-0.21	-0.12	0.30	0.35	0.28	0.08	0.52*	0.09	0.30	0.17	0.34	0.43	-0.20
MPSGraz500	-0.06	-0.26	-0.22	-0.12	0.73**	0.48*	0.23	-0.16	-0.67**	-0.37	-0.12	0.24	-0.28	0.17	-0.20	-0.08	-0.23	-0.20	-0.13
NPGraz1000	0.51*	0.55*	0.19	0.30	-0.36	-0.56*	-0.35	-0.39	0.21	0.32	0.27	0.23	0.29	0.28	0.06	0.44*	0.23	0.61**	-0.16
MPSGraz1000	-0.26	-0.39	-0.17	-0.19	0.45*	0.72**	0.55*	0.31	-0.34	-0.56*	-0.47*	-0.20	-0.23	-0.02	-0.13	-0.23	-0.23	-0.26	-0.09
NPGraz1500	0.46*	0.58**	0.42	0.54*	-0.15	-0.32	-0.34	-0.31	0.05	0.08	0.12	0.01	0.23	0.40	-0.14	0.61**	0.12	0.71**	0.01
MPSGraz1500	-0.49*	-0.69**	-0.56*	-0.67**	0.32	0.52*	0.55*	0.44	-0.19	-0.23	-0.25	-0.06	-0.11	-0.31	0.17	-0.48*	-0.20	-0.54*	-0.15
NPGraz2000	0.56*	0.64**	0.43	0.68**	0.21	0.12	-0.03	-0.28	-0.31	-0.41	-0.21	-0.10	-0.04	0.62**	-0.32	0.76**	-0.04	0.77**	-0.19
MPSGraz2000	-0.62**	-0.73**	-0.49*	-0.76**	-0.21	-0.03	0.19	0.62**	0.32	0.36	0.08	-0.20	0.17	-0.60**	0.45*	-0.62**	-0.01	-0.63**	0.11
NPCult500	0.34	0.21	0.18	0.13	0.53*	0.37	0.28	-0.14	-0.56*	-0.46*	-0.38	0.09	-0.25	0.59**	-0.55*	0.45*	-0.34	0.49*	-0.33
MPSCult500	-0.46*	-0.34	-0.40	-0.26	-0.66**	-0.46*	-0.38	0.09	0.71**	0.63**	0.62**	0.06	0.54*	-0.57**	0.72**	-0.42	0.35	-0.37	0.19
NPCult1000	0.19	-0.19	-0.34	-0.20	0.56**	0.49*	0.35	0.19	-0.59**	-0.43	-0.16	-0.07	-0.09	0.19	-0.05	0.15	-0.18	-0.03	-0.36
MPSCult1000	-0.21	0.10	0.13	0.07	-0.63**	-0.66**	-0.51*	-0.24	0.65**	0.64**	0.44	0.20	0.44	-0.24	0.35	-0.17	0.36	0.04	0.35
NPCult1500	0.27	-0.17	-0.21	-0.14	0.23	0.29	0.48*	0.50*	-0.29	-0.19	-0.34	-0.43	0.07	0.25	-0.01	0.39	-0.37	0.41	-0.48*
MPSCult1500	-0.31	0.07	0.01	0.05	-0.50*	-0.51*	-0.67**	-0.49*	0.54*	0.46*	0.65**	0.47*	0.25	-0.40	0.31	-0.42	0.49*	-0.41	0.47*
NPCult2000	0.05	0.24	0.00	0.11	-0.44*	-0.35	-0.22	-0.05	0.40	0.23	0.22	-0.02	0.55*	-0.23	0.41	0.07	0.51*	0.29	0.12
MPSCult2000	-0.06	-0.27	-0.20	-0.15	0.55*	0.30	0.10	-0.17	-0.50*	-0.17	0.02	0.28	-0.26	0.23	-0.20	-0.13	-0.30	-0.30	-0.12

	NPVeg2000	MPSVeg2000	NPGraz500	MPSGraz500	NPGraz1000	MPSGraz1000	NPGraz1500	MPSGraz1500	NPGraz2000	MPSGraz2000	NPCult500	MPSCult500	NPCult1000	MPSCult1000	NPCult1500	MPSCult1500	NPCult2000	MPSCult2000
Veg500																		
Veg1000																		
Veg1500																		
Veg2000																		
Graz500																		
Graz1000																		
Graz1500																		
Graz2000																		
Cult500																		
Cult1000																		
Cult1500																		
Cult2000																		
PatchArea																		
NPVeg500																		
MPSVeg500																		
NPVeg1000																		
MPSVeg1000																		
NPVeg1500																		
MPSVeg1500																		
NPVeg2000	1.00																	
MPSVeg2000	-0.59**	1.00																
NPGraz500	0.45*	-0.16	1.00															
MPSGraz500	-0.24	0.04	-0.50*	1.00														
NPGraz1000	0.58**	-0.19	0.76**	-0.47*	1.00													
MPSGraz1000	-0.12	-0.14	-0.48*	0.43	-0.76**	1.00												
NPGraz1500	0.69**	-0.05	0.41	-0.39	0.69**	-0.57**	1.00											
MPSGraz1500	-0.48*	-0.18	-0.42	0.45*	-0.71**	0.73**	-0.91**	1.00										
NPGraz2000	0.83**	-0.21	0.14	-0.06	0.46*	-0.15	0.74**	-0.60**	1.00									
MPSGraz2000	-0.71**	0.10	-0.18	-0.06	-0.47*	0.18	-0.66**	0.63**	-0.88**	1.00								
NPCult500	0.27	-0.24	0.14	0.25	0.06	0.08	0.26	-0.15	0.19	-0.32	1.00							
MPSCult500	-0.16	0.14	0.25	-0.34	0.03	-0.18	-0.15	0.04	-0.28	0.34	-0.73**	1.00						
NPCult1000	-0.05	-0.19	-0.20	0.48*	-0.34	0.35	-0.28	0.41	-0.01	0.03	0.20	-0.30	1.00					
MPSCult1000	0.10	0.20	0.46*	-0.47*	0.50*	-0.49*	0.37	-0.45*	0.00	-0.02	-0.23	0.49*	-0.89**	1.00				
NPCult1500	0.35	-0.45*	0.07	0.02	0.15	0.04	0.16	0.06	0.22	0.04	0.06	-0.27	0.49*	-0.44	1.00			
MPSCult1500	-0.30	0.44	0.12	-0.18	0.01	-0.23	-0.03	-0.19	-0.21	0.01	-0.28	0.61**	-0.48*	0.57**	-0.88**	1.00		
NPCult2000	0.48*	-0.09	0.46*	-0.47*	0.43	-0.20	0.53*	-0.32	0.40	-0.25	-0.19	0.25	-0.11	0.31	0.17	0.08	1.00	
MPSCult2000	-0.38	0.10	-0.31	0.73**	-0.34	0.18	-0.45*	0.31	-0.31	0.12	0.22	-0.16	0.18	-0.21	-0.21	0.04	-0.85**	1.00

Table A3.2. Correlation table for vegetation structural variables used in multiple regression analyses.

Brigalow	Trees20	Trees1020	Trees10	Shrubs2	Shrubs12	Shrubs1	ForbsHerbs	Grasses	Bareground	Litter	Logs
Trees20	1										
Trees1020	0.55**	1									
Trees10	0.45**	0.43**	1								
Shrubs2	0.83**	0.72**	0.39*	1							
Shrubs12	0.15	0.13	0.28	0.13	1						
Shrubs1	0.40*	0.38*	0.51**	0.32*	0.11	1					
ForbsHerbs	0.65**	0.70**	0.68**	0.57**	0.22	0.64**	1				
Grasses	-0.09	-0.11	-0.11	-0.14	-0.36*	-0.16	0.07	1			
Bareground	-0.41**	-0.47**	-0.25	-0.39*	0.26	-0.15	-0.52**	-0.63**	1		
Litter	0.46**	0.60**	0.34*	0.59**	0.08	0.25	0.33*	-0.53**	-0.26	1	
Logs	0.72**	0.83**	0.65**	0.83**	0.17	0.40*	0.72**	-0.12	-0.49**	0.62**	1

Matrix	Shrubs1	ForbsHerbs	Grasses	Bareground	Litter
Shrubs1	1				
ForbsHerbs	0.180	1			
Grasses	-0.16	0.46*	1		
Bareground	0.090	-0.39	-0.88**	1	
Litter	0.120	-0.390	-0.58**	0.18	1

Appendix 4. Mean abundance and frequency data for all recorded plant species across experimental treatments.

Table A4.1. List of all plant species recorded during formal surveys, their functional group classifications, mean abundance and number of sites in which species were recorded (frequency) at edge and core sampling sites in Brigalow and the matrix. Species were assigned to functional groups based on a combination of the following attributes: 1) monocot (M) or dicot (D), 2) native (N) or exotic (E), and 3) annual (A) or perennial (P).

Species name	Functional group	Brigalow Core		Brigalow Edge		Matrix Edge		Matrix Core	
		Number of sites	Mean abundance	Number of sites	Mean abundance	Number of sites	Mean abundance	Number of sites	Mean abundance
Abutilon otocarpum	PND	15	0.32	14	0.47	1	0.20	0	-
Abutilon oxycarpum	PND	4	0.60	2	0.15	0	-	0	-
Acacia harpophylla	PND	1	0.30	0	-	0	-	0	-
Alectryon	PND	1	0.20	1	0.10	0	-	0	-
Alternathera denticulata	PND	0	-	1	0.20	1	0.20	0	-
Amaranthus hybridus	AED	1	0.50	6	0.52	3	0.17	3	0.30
Amaranthus macrocarpus	AND	0	-	2	0.15	3	1.17	4	0.30
Ancistrachne uncinulata	PNM	15	2.19	6	1.28	0	-	0	-
Anoda cristata	PED	0	-	0	-	1	1.70	2	1.35
Apium leptophyllum	AED	0	-	0	-	0	-	1	0.10
Apophyllum anomalum	PND	2	0.60	1	1.50	1	0.70	0	-
Aristida latifolia	PNM	0	-	2	0.25	1	8.60	2	4.00
Aristida ramosa	PNM	0	-	1	0.80	1	0.20	0	-
Atriplex elacophylla	PND	2	0.25	3	0.73	0	-	1	0.10
Atriplex muelleri	PND	0	-	1	3.60	2	0.30	0	-
Atriplex semibaccata	PND	3	0.67	5	0.68	2	0.30	1	0.10
Bidens pilosa	AND	1	0.70	2	0.25	0	-	0	-
Boerhavia diffusa	AND	11	0.38	9	0.29	3	0.17	0	-
Bothriochloa decipiens	PNM	0	-	0	-	2	4.30	1	0.50
Brachiaria eruciformis	AEM	0	-	1	0.20	2	0.80	2	3.85
Brachyscome curvicarpa	PND	2	0.10	0	-	2	0.40	0	-

Species name	Functional group	Brigalow Core		Brigalow Edge		Matrix Edge		Matrix Core	
		Number of sites	Mean abundance	Number of sites	Mean abundance	Number of sites	Mean abundance	Number of sites	Mean abundance
Brassica chinensis	AED	0	-	1	0.20	0	-	0	-
Calotis cuneata	PND	5	0.12	4	0.15	1	0.10	1	0.20
Calotis lappulacea	PND	0	-	0	-	1	0.40	0	-
Capparis lasiantha	PND	10	0.39	4	0.48	0	-	0	-
Capparis sarmentosa	PND	1	0.10	0	-	0	-	0	-
Cardiospermum halicacabum	AED	7	0.39	8	0.15	0	-	0	-
Carissa ovata	PND	3	2.10	1	1.80	0	-	0	-
Cenchrus ciliaris	PEM	0	-	1	1.50	0	-	0	-
Cheilanthes sieberi	PND	10	0.20	1	0.40	0	-	0	-
Chenopodium carinatum	PND	2	1.05	2	2.70	2	1.00	3	2.20
Chenopodium cristatum	PND	1	0.10	1	0.30	0	-	0	-
Chenopodium trigonon	PND	9	6.03	5	5.42	0	-	0	-
Chloris divaricata	PNM	10	2.11	7	1.51	2	7.35	2	7.45
Chloris gayana	PEM	0	-	1	1.20	0	-	1	0.50
Chloris truncata	PNM	0	-	0	-	1	1.10	1	0.30
Chloris ventricosa	PNM	10	0.70	11	1.32	2	6.20	1	3.20
Chloris virgata	ANM	0	-	1	0.30	1	0.70	2	1.35
Commelina cyanea	PND	18	0.74	17	0.36	1	0.10	2	0.90
Convolvulus arvensis	PED	0	-	0	-	0	-	1	0.10
Cymbopogon	PNM	1	1.00	0	-	0	-	0	-
Cynodon dactylon	PNM	10	8.99	18	8.31	7	18.93	6	28.90
Cyperus gracilis	PNM	17	0.56	15	0.63	1	2.90	1	0.10
Cyperus rigidellus	PNM	1	0.10	3	0.87	3	2.17	2	4.05
Dactyloctenium radulans	ANM	0	-	1	1.00	5	15.14	4	9.25
Danthonia longifolia	PNM	4	0.45	4	0.43	0	-	0	-
Danthonia tenuior	PNM	1	0.10	4	0.23	0	-	0	-
Datura ferox	AED	1	0.10	0	-	1	0.10	0	-
Dianella	PND	3	0.13	2	0.15	0	-	0	-
Dichanthium sericeum	PNM	0	-	0	-	4	26.60	3	26.90

Species name	Functional group	Brigalow Core		Brigalow Edge		Matrix Edge		Matrix Core	
		Number of sites	Mean abundance	Number of sites	Mean abundance	Number of sites	Mean abundance	Number of sites	Mean abundance
Dichondra repens	PND	0	-	0	-	1	0.40	1	0.80
Digitaria brownii	PNM	7	1.59	14	0.77	3	4.10	2	0.50
Digitaria eriantha	PEM	0	-	0	-	0	-	1	8.00
Digitaria sanguinalis	AEM	1	0.40	1	0.80	0	-	0	-
Echinochloa colona	AEM	0	-	0	-	4	1.15	5	2.78
Einadia nutans	PND	18	3.31	19	3.11	6	0.72	5	0.38
Eleusine tristachya	AEM	1	0.10	0	-	0	-	0	-
Enchylaena tomentosa	PND	17	1.58	18	2.28	2	1.00	0	-
Enneapogon nigricans	PNM	0	-	1	0.10	1	2.20	1	1.50
Eragrostis brownii	PNM	1	1.00	1	0.60	1	0.10	0	-
Eragrostis cilianensis	AEM	0	-	0	-	4	4.83	3	6.00
Eragrostis minor	AEM	0	-	0	-	1	0.80	1	0.10
Eriochloa pseudoacrotricha	PNM	0	-	3	0.30	4	1.40	3	3.10
Eromocitrus glauca	PND	3	0.10	1	0.10	1	0.20	0	-
Euphorbia drummondii	PND	0	-	1	0.70	4	0.28	7	1.69
Eustrephus latifolius	PND	1	0.10	0	-	0	-	0	-
Evolvulus alsinoides	PND	0	-	1	0.30	0	-	0	-
Glycine clandestina	PND	1	0.70	1	0.30	0	-	0	-
Glycine tabacina	PND	4	0.13	2	0.20	0	-	1	0.10
Hibiscus trionum	AND	0	-	0	-	1	0.80	3	0.43
Homophilis belsonii	PNM	3	0.90	9	1.18	0	-	0	-
Hypoestes floribunda	PND	3	6.10	1	1.20	0	-	0	-
Jasminum didymum (lineare)	PND	12	0.56	11	0.22	0	-	0	-
Justicia procumbens	PND	3	0.40	5	0.16	0	-	1	0.10
Lepidium hyssopifolium	AND	0	-	2	0.10	3	0.27	0	-
Leptochloa ciliolata	PNM	6	1.08	5	0.48	0	-	0	-
Leptochloa decipiens	PNM	1	0.70	1	2.10	0	-	0	-
Leptochloa divaricatissima	PND	0	-	3	0.93	2	5.65	1	0.30
Lippia nodiflora	PED	0	-	1	0.90	1	19.10	2	0.70

Species name	Functional group	Brigalow Core		Brigalow Edge		Matrix Edge		Matrix Core	
		Number of sites	Mean abundance	Number of sites	Mean abundance	Number of sites	Mean abundance	Number of sites	Mean abundance
Lycium ferosissimum	PED	2	0.55	1	0.10	1	0.70	0	-
Maireana enchylaenoides	PND	3	0.50	5	1.42	2	0.90	0	-
Malva parviflora	PED	1	0.20	1	0.10	2	0.20	2	0.10
Malvastrum americanum	PED	3	0.30	3	1.53	3	0.57	3	0.27
Malvastrum coromandelianum	PED	3	0.33	7	0.16	1	0.20	1	0.40
Medicago minima	AED	1	0.20	2	0.30	2	1.25	2	1.55
Medicago polymorpha (vulgaris)	AED	0	-	1	0.20	3	0.13	4	0.13
Myoporum debile	PND	6	0.48	9	0.39	0	-	0	-
Notolaea	PND	1	0.20	0	-	0	-	0	-
Nyssanthes erecta	PND	5	0.10	4	0.25	0	-	0	-
Opuntia tomentosa	PED	7	0.11	4	0.15	2	0.15	2	0.15
Oxalis corriculata	PND	15	0.35	18	0.30	7	0.31	5	0.24
Panicum buncei	PNM	0	-	1	0.30	3	0.37	1	0.60
Panicum decompositum	PNM	0	-	0	-	1	1.00	1	0.20
Panicum maximum	PEM	8	5.88	6	10.75	3	7.03	1	16.40
Panicum miliaceum	AEM	0	-	0	-	1	10.80	1	13.00
Panicum queenslandicum	PNM	1	0.10	1	0.10	1	1.40	1	0.50
Parsonsia eucalyptophylla	PND	1	0.10	1	0.10	0	-	0	-
Parsonsia lanceolata	PND	11	1.02	9	0.37	0	-	1	0.10
Paspalidium caespitosum	PNM	6	1.82	7	4.23	2	5.50	1	0.10
Paspalidium constrictum	PNM	4	4.15	3	7.60	0	-	1	4.30
Paspalidium criniforme	PNM	18	3.13	12	4.70	1	1.10	0	-
Paspalidium disjunctum	PNM	0	-	0	-	1	0.10	0	-
Paspalidium globoideum	PNM	0	-	2	3.80	0	-	0	-
Phalaris canariensis	AEM	0	-	0	-	1	27.50	1	40.80
Pimelea glauca	PND	0	-	0	-	0	-	1	0.30
Plantago debilis	PND	0	-	1	0.10	0	-	0	-
Plectranthus parviflorus	PND	12	0.57	8	0.50	1	0.10	0	-
Portulaca oleracea	AND	14	0.31	13	0.54	14	1.45	8	1.33

Species name	Functional group	Brigalow Core		Brigalow Edge		Matrix Edge		Matrix Core	
		Number of sites	Mean abundance	Number of sites	Mean abundance	Number of sites	Mean abundance	Number of sites	Mean abundance
Portulaca pilosa	AED	1	0.30	1	1.60	1	1.10	1	0.80
Pseuderanthemum variabile	PND	5	0.28	2	0.35	0	-	0	-
Raphanus raphanistrum	AED	0	-	0	-	2	0.10	3	0.33
Rapistrum rugosum	AED	0	-	1	0.20	2	0.40	3	0.17
Rhynchosia minima (australis)	PND	0	-	0	-	0	-	1	1.20
Ruellia australis	PND	4	0.25	1	0.60	0	-	0	-
Salsola kali	PND	0	-	6	1.42	3	1.63	1	0.10
Salvia reflexa	AED	1	0.10	9	0.69	13	0.48	8	0.25
Schkuhria pinnata	AED	0	-	0	-	1	1.50	1	1.20
Sclerolaena muricata	PND	0	-	5	0.26	3	0.63	2	0.90
Sclerolaena tetracuspis	PND	16	1.58	15	3.79	3	0.93	2	0.80
Sida cunninghamii	PND	10	0.20	12	0.17	0	-	0	-
Sida subspicata	PND	3	2.03	2	0.45	1	13.90	1	0.40
Sigesbeckia orientalis	AND	1	0.50	0	-	0	-	0	-
Silybum marianum	AED	1	0.20	1	0.10	1	0.10	0	-
Solanum nigrum	AED	0	-	1	0.20	0	-	0	-
Solanum parviflorum	PND	14	0.54	13	1.15	0	-	0	-
Solanum semiarmatum	PND	4	0.23	2	0.15	0	-	0	-
Sonchus oleraceus	AED	6	0.13	7	0.13	3	0.47	4	0.33
Sorghum sp.	AEM	0	-	0	-	5	7.40	4	7.90
Sporobolus caroli	PNM	6	0.62	7	0.44	1	0.60	2	0.10
Sporobolus creber	PNM	0	-	0	-	0	-	1	0.50
Stipa verticillata	PNM	13	0.52	12	0.80	2	0.10	3	1.57
Tetragonia tetragonioides	AND	16	1.31	18	2.51	9	0.36	4	0.15
Tragus australianus	ANM	0	-	4	0.48	2	0.65	3	0.60
Trianthema portulacastrum	AED	0	-	0	-	3	1.07	0	-
Trianthema triquetra	AND	2	0.15	3	0.37	3	0.50	1	0.50
Tribulus terrestris	AND	10	0.25	14	0.35	10	1.87	8	0.31
Trifolium dubium	AED	0	-	0	-	1	0.10	0	-

Species name	**Functional group**	**Brigalow Core**		**Brigalow Edge**		**Matrix Edge**		**Matrix Core**	
		Number of sites	**Mean abundance**	**Number of sites**	**Mean abundance**	**Number of sites**	**Mean abundance**	**Number of sites**	**Mean abundance**
Urochloa mosambicensis	PEM	3	0.33	1	0.20	0	-	0	-
Urochloa panicoides	AEM	3	0.93	9	0.68	12	3.92	12	8.48
Verbena officianalis	PED	0	-	0	-	3	0.37	3	0.30
Verbena tenuisecta	PED	0	-	3	0.50	4	0.35	2	1.05
Vittadinia diffusa	PND	0	-	0	-	1	0.10	0	-
Vittadinia pterochaeta	PND	0	-	1	0.20	2	0.25	1	1.00
Vittadinia sulcata	PND	1	0.50	2	0.15	2	0.20	0	-
Zaleya galericulata	AND	0	-	0	-	1	1.50	0	-
Zea sp.	AEM	0	-	0	-	1	0.90	1	0.10
Zinnia peruviana	AED	0	-	0	-	1	0.10	0	-
Zygophyllum apiculatum	PND	5	0.22	7	0.29	0	-	0	-

Appendix 5. Functional group classifications for plant species

Table A5.1. Functional group classifications for plant species recorded across all study sites. Functional groups as per Appendix 4

Annual Dicot	Annual Monocot	Perennial Dicot	Perennial Monocot
Native	**Native**	**Native**	**Native**
Amaranthus macrocarpus	*Chloris virgata*	*Abutilon otocarpum*	*Ancistrachne uncinulata*
Bidens pilosa	*Dactyloctenium radulans*	*Abutilon oxycarpum*	*Aristida latifolia*
Boerhavia diffusa	*Tragus australianus*	*Acacia harpophylla*	*Aristida ramosa*
Hibiscus trionum	**Exotic**	*Alectryon* sp.	*Bothriochloa decipiens*
Lepidium hyssopifolium	*Brachiaria eruciformis*	*Alternathera denticulata*	*Chloris divaricata*
Portulaca oleracea	*Digitaria sanguinalis*	*Apophyllum anomalum*	*Chloris truncata*
Sigesbeckia orientalis	*Echinochloa colona*	*Atriplex elacophylla*	*Chloris ventricosa*
Tetragonia tetragonioides	*Eleusine tristachya*	*Atriplex muelleri*	*Cymbopogon*
Trianthema triquetra	*Eragrostis cilianensis*	*Atriplex semibaccata*	*Cynodon dactylon*
Tribulus terrestris	*Eragrostis minor*	*Brachyscome curvicarpa*	*Cyperus gracilis*
Zaleya galericulata	*Panicum miliaceum*	*Calotis cuneata*	*Cyperus rigidellus*
Exotic	*Phalaris canariensis*	*Calotis lappulaceae*	*Danthonia longifolia*
Amaranthus hybridus	*Sorghum* sp.	*Capparis lasiantha*	*Danthonia tenuior*
Apium leptophyllum	*Urochloa panicoides*	*Capparis sarmentosa*	*Dichanthium sericeum*
Brassica chinensis	*Zea* sp.	*Carissa ovata*	*Digitaria brownii*
Cardiospermum halicacabum		*Cheilanthes sieberi*	*Enneapogon nigricans*
Datura Ferox		*Chenopodium carinatum*	*Eragrostis brownii*
Medicago minima		*Chenopodium cristatum*	*Eriochloa pseudoacrotricha*
Medicago polymorpha (vulgaris)		*Chenopodium trigonon*	*Homophilis belsonii*
Portulaca pilosa		*Commelina cyanea*	*Leptochloa ciliolata*
Raphanus raphanistrum		*Dianella* sp.	*Leptochloa decipiens*
Rapistrum rugosum		*Dichondra repens*	*Leptochloa divaricatissima*
Salvia reflexa		*Einadia nutans*	*Panicum buncei*
Schkuhria pinnata		*Enchylaena tomentosa*	*Panicum decompositum*
Silybum marianum		*Eromocitrus glauca*	*Panicum queenslandicum*
Solanum nigrum		*Euphorbia drummondii*	*Paspalidium caespitosum*
Sonchus oleraceus		*Eustrephus latifolius*	*Paspalidium constrictum*
Trianthema portulacastrum		*Evolvulus alsinoides*	*Paspalidium criniforme*
Trifolium dubium		*Glycine clandestina*	*Paspalidium disjunctum*
Zinnia peruviana		*Glycine tabacina*	*Paspalidium globoideum*
		Hypoestes floribunda	*Sporobolus caroli*
		Jasminum didymum (lineare)	*Sporobolus creber*
		Justicia procumbens	*Stipa verticillata*
		Maireana enchylaenoides	**Exotic**
		Myoporum debile	*Cenchrus ciliaris*
		Notolaea	*Chloris gayana*
		Nyssanthes erecta	*Digitaria eriantha*
		Oxalis corriculata	*Panicum maximum*
		Parsonsia eucalyptophylla	*Urochloa mosambicensis*
		Parsonsia lanceolata	
		Pimelea glauca	
		Plantago debilis	
		Plectranthus parviflorus	
		Pseuderanthemum variabile	
		Rhynchosia minima (australis)	
		Ruellia australis	
		Salsola kali	
		Sclerolaena muricata	
		Sclerolaena tetracuspis	
		Sida cunninghamii	
		Sida subspicata	
		Solanum parviflorum	
		Solanum semiarmatum	
		Vittadinia diffusa	
		Vittadinia pterochaeta	
		Vittadinia sulcata	
		Zygophyllum apiculatum	
		Exotic	
		Anoda cristata	
		Convolvulus arvensis	
		Lippia nodiflora	
		Lycium ferosissimum	
		Malva parviflora	
		Malvastrum americanum	
		Malvastrum coromandelianum	
		Opuntia tomentosa	
		Verbena officianalis	
		Verbena tenuisecta	

Appendix 6. Results of multivariate analyses (nMDS ordination, ANOSIM and SIMPER) on percentage plant cover data at core and edge in each land management category.

An nMDS ordination of percentage cover data separated the four land management categories, with the distance between points reflecting the similarity of floristic composition (Clarke 1993). A gradient is evident on the ordination from Brigalow sites (on the right of the diagram) through grassland (Grass$_U$ and Grass$_P$) to cultivation (on the left) (Figure A6.1). Separate groupings of core and edge samples within the same land management category were not obvious (Figure A6.1).

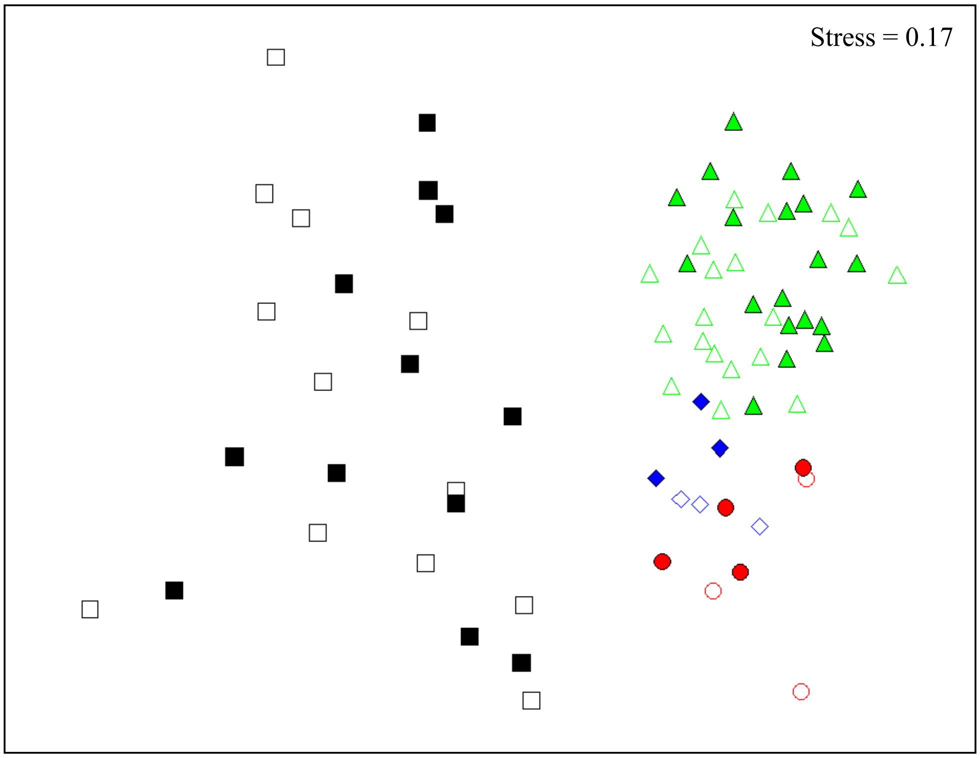

Figure A6.1. Two-dimensional ordination (nMDS) of percent plant cover data, showing core (shaded) and edge (open) within each land management category ▲ = Brigalow core, △ = Brigalow edge, ◆ = Grass$_U$ core, ◇ = Grass$_U$ edge, ● = Grass$_P$ core, ○ = Grass$_P$ edge, ■ = Cultivation core, □ = Cultivation edge.

Two-way crossed Analysis of Similarity (ANOSIM) showed no significant differences in herbaceous plant community composition between core and edge across all land management categories (Global *R* = 0.048, *P* = 0.075). However, there were significant differences between land management categories (Global *R* = 0.749, *P* = 0.001). Pairwise tests showed significant differences (P ≤ 0.001) between all land management categories except Grass_U and Grass_P (Table A6.1).

Table A6.1. Summary of Analysis of Similarity (ANOSIM) on percent plant cover data. Values are R statistics (from pairwise tests) with significance level indicated.

	Brigalow	**GRASS_U**	**GRASS_P**
GRASS_U	0.721**	-	-
GRASS_P	0.891**	0.296^{ns}	-
Cultivation	0.874**	0.289*	0.418**

**p < 0.001, *p < 0.05, ns = not significant.

Species that contributed up to 50% of the Bray-Curtis similarity within each land management category are listed in Table A6.2.

Table A6.2. Species contributing up to 50% of Bray-Curtis similarity for each land management category for percentage plant cover data. Species are listed in decreasing order of their contribution to similarity.

LMC	Species	Functional group	Avg abundance	Cumulative %
Brigalow	Average similarity = 27.12			
	Cynodon dactylon	PNM	6.3	15.56
	Einadia nutans	PND	3.12	28.52
	Paspalidium criniforme	PNM	2.97	41.31
	Sclerolaena tetracuspis	PND	2.16	50.43
Grass_U	Average similarity = 42.4			
	Cynodon dactylon	PNM	25.82	67.61
Grass_P	Average similarity = 33.1			
	Dichanthium sericeum	PNM	26.64	63.29
Cultivation	Average similarity = 9.23			
	Echinochloa colona	AEM	0.77	20.94
	Sorghum sp.	AEM	2.86	39.56
	Urochloa panicoides	AEM	1.47	56.48

P = perennial, A = annual, N = native, E = exotic, M = monocot, D = dicot.

Appendix 7. Average dissimilarity between land management categories.

Table A7.1. Results of a SIMPER analysis on plant frequency data. Average dissimilarity between land management categories (LMC) and the average abundance of species that contributed up to 50% of the dissimilarity between land management categories. Species are listed in decreasing order of their importance in discriminating the two sets of samples.

Species	**Average abundance**		**Cumulative %**
Average dissimilarity = 98.29	**Brigalow**	**Cultivation**	
Cynodon dactylon	6.3	0.15	10.79
Paspalidium criniforme	2.97	0	17.23
Einadia nutans	3.12	0	23.09
Panicum maximum	2.93	0	28.61
Sorghum sp.	0	2.86	33.59
Dactyloctenium radulans	0.03	4.67	38.14
Sclerolaena tetracuspis	2.16	0	42.59
Chenopodium trigonon	2.14	0	46.74
Enchylaena tomentosa	1.79	0	50.37
Average dissimilarity = 84.60	**Brigalow**	**GrassU**	**Cumulative %**
Cynodon dactylon	6.3	25.88	25.88
Urochloa panicoides	0.23	16.67	42.38
Lippia nodiflora	0.02	3.35	46.14
Paspalidium criniforme	2.97	0.18	49.43
Panicum maximum	2.93	0	52.65
Average dissimilarity = 96.72	**Cultivation**	**GrassU**	**Cumulative%**
Cynodon dactylon	0.15	25.82	34.28
Urochloa panicoides	1.47	16.67	51.85
Average dissimilarity = 90.18	**Brigalow**	**GrassP**	**Cumulative %**
Dichanthium sericeum	0	26.64	28.4
Cynodon dactylon	6.3	21.07	47.92
Panicum maximum	2.93	5.34	54.18
Average dissimilarity = 98.05	**Cultivation**	**GrassP**	**Cumulative%**
Dichanthium sericeum	0	26.64	33.03
Cynodon dactylon	0.15	21.07	54.83
Average dissimilarity = 80.15	**GrassU**	**GrassP**	**Cumulative%**
Dichanthium sericeum	0.08	26.64	24.75
Cynodon dactylon	25.82	21.07	46.41
Urochloa panicoides	16.67	1.93	59.36

Appendix 8. Bird species accumulation

Attempts to comprehensively census birds are often confounded by factors such as behavioural responses of certain species, effects of habitat complexity and issues associated with species identification (Watson 2003). However, inferences can be made providing that the level of completeness is equivalent across all sites being sampled. Levels of completeness are generally constrained by resource (time and money) availability. Formal decisions about when to stop are typically based on effort-based or results-based stopping rules (Watson 2003). Effort-based rules are usually limited by the amount of time spent sampling, while results-based rules use the data to determine a robust stopping rule, which is applied during sampling.

In this study, a combination of the two methods was used, based on average accumulation of species across Brigalow and matrix sites. Briefly, ten randomly generated permutations of species richness data were derived from the 5 surveys in the same site (Field *et al*. 2002). Random permutations were generated using 'macro' codes in Visual Basic Editor (Microsoft Excel). The permutation procedure re-orders data from surveys at the same site, so that a mean of the number of new species per survey can be calculated for that site. This essentially reduces bias due to ordering of repeat visits by evening out the effects of high or low species richness counts of individual surveys that may disproportionately affect the species accumulation curve.

To determine optimum sampling efficiency (i.e. the number of surveys needed to detect the maximum number of bird species per site), a stopping rule for the number of surveys was determined using data from Brigalow and matrix surveys at five pilot study sites (sites were 1, 2, 3, 4 and 9). Based on permuted data for each site, the mean average increase in species richness per survey, across 5 of the pilot sites, was determined (Figure A8.1). Based on these preliminary data, a stopping rule was applied when the mean increase of new species per survey fell below 2, after 3 surveys (Figure A8.1). The remaining sites were surveyed three times, with only the first three of the samples used in the pilot analysis used in the subsequent analyses.

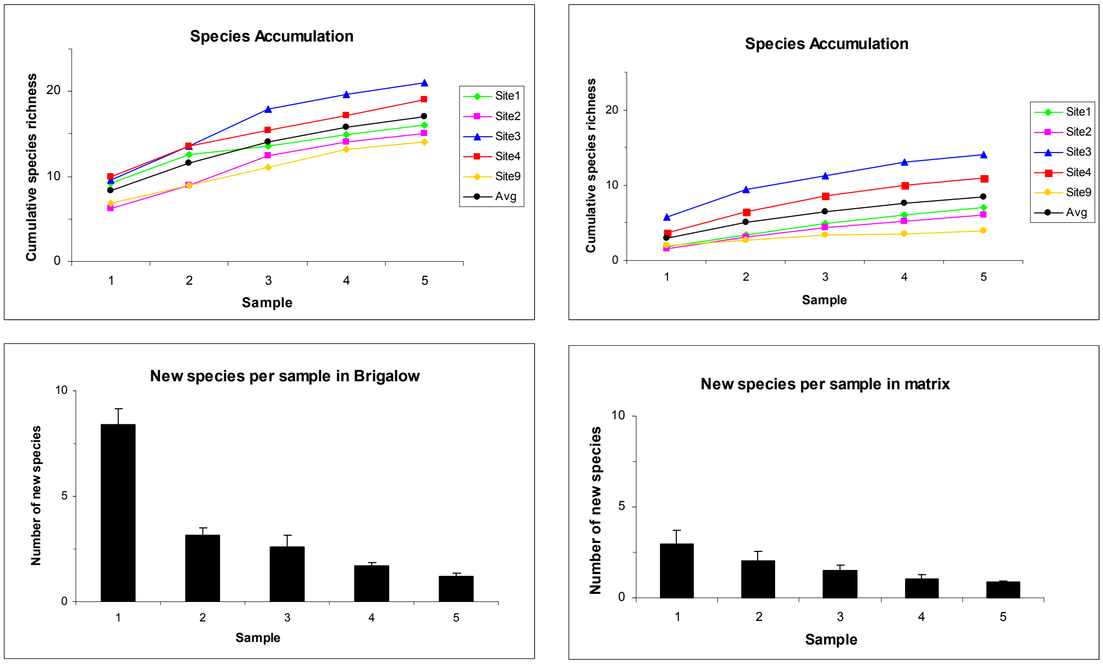

Figure A8.1. Species accumulation curves for the five Brigalow (top left) and five matrix (top right) pilot surveys. Bar charts below show the mean number of new bird species recorded per survey. Error bars in lower charts are standard errors.

Appendix 9. Mean abundance and frequency of all bird species in all land management categories

Table A9.1. List of bird species recorded during formal surveys, their functional group classification and their mean abundance and number of Brigalow and matrix sites recorded. * denotes bird species not recorded during formal surveys. Foraging guilds: 1 = Ground-foraging insectivore, 2 = Raptor, 3 = Granivore, 4 = Canopy-foraging insectivore, 5 = Open grassland species, 6 = Nectarivore/insectivore, 7 = Frugivore, 8 = Understorey species.

			Brigalow		GrassU		GrassP		Cultivation	
Family **Scientific Name**	**Common Name**	**Functional group**	**# Sites (n=20)**	**Average Abund**	**# Sites (n=3)**	**Average Abund**	**# Sites (n=4)**	**Average Abund**	**# Sites (n=20)**	**Average Abund**
Phalacrocoracidae										
Phalacrocorax melanoleucos	Little Pied Cormorant*	-	-	-	-	-	-	-	-	-
Anatidae										
Chenonetta jubata	Australian Wood Duck*	-	-	-	-	-	-	-	-	-
Anas gracilis	Grey Teal*	-	-	-	-	-	-	-	-	-
Anas superciliosa	Pacific Black Duck*	-	-	-	-	-	-	-	-	-
Dendrocygna eytoni	Plumed Whistling Duck*	-	-	-	-	-	-	-	-	-
Accipitridae										
Elanus axillaris	Black-shouldered Kite	2	0	-	0	-	0	-	1	0.08
Circus assimilis	Spotted Harrier	2	0	-	0	-	0	-	3	0.23
Aquila audax	Wedge-tailed Eagle*	-	-	-	-	-	-	-	-	-
Falconidae										
Falco cenchroides	Australian Kestrel	2	0	-	1	0.33	0	-	3	0.31
Falco subniger	Black Falcon*	-	-	-	-	-	-	-	-	-
Falco berigora	Brown Falcon	2	1	2.00	0	-	0	-	0	-
Falco peregrinus	Peregrine Falcon*	-	-	-	-	-	-	-	-	-
Phasianidae										
Coturnix ypsilophora	Brown Quail	5	0	-	0	-	0	-	1	0.15
Ardeidae										
Ardea alba	Great Egret*	-	-	-	-	-	-	-	-	-

Family Scientific Name	Common Name	Functional group	Brigalow # Sites (n=20)	Brigalow Average Abund	GrassU # Sites (n=3)	GrassU Average Abund	GrassP # Sites (n=4)	GrassP Average Abund	Cultivation # Sites (n=20)	Cultivation Average Abund
Egretta novaehollandiae	White-faced Heron	1	0	-	1	0.67	0	-	0	-
Threskiornithidae										
Threskionis spinicollis	Straw-necked Ibis	1	0	-	0	-	0	-	2	0.46
Platalea flavipes	Yellow-billed Spoonbill*	-	-	-	-	-	-	-	-	-
Charadriidae										
Vanellus miles	Masked Lapwing*	-	-	-	-	-	-	-	-	-
Otidae										
Ardeotis australis	Australian Bustard*	-	-	-	-	-	-	-	-	-
Columbidae										
Geopelia humeralis	Bar-shouldered Dove	3	3	1.33	0	-	0	-	0	-
Ocyphaps lophotes	Crested Pigeon	3	20	8.10	3	3.67	0	-	6	1.62
Geopelia striata	Peaceful Dove	3	0	-	0	-	0	-	1	0.15
Cacatuidae										
Nymphicus hollandicus	Cockatiel	3	17	8.82	0	-	0	-	1	0.54
Cacatua roseicapilla	Galah	3	17	4.94	2	2.33	1	1.50	3	0.46
Cacatua sanguinea	Little Corella	3	1	2.00	0	-	0	-	1	0.23
Cacatua galerita	Sulphur-crested Cockatoo	3	1	5.00	0	-	0	-	0	-
Psittacidae										
Northiella haematogaster	Blue Bonnet	3	0	-	1	0.67	1	0.50	0	-
Platycercus adscitus	Pale-headed Rosella	3	16	4.69	1	1.33	0	-	0	-
Psephotus haematonotus	Red-rumped Parrot	3	12	8.67	1	1.67	0	-	2	0.54
Aprosmictus erythropterus	Red-winged Parrot*	-	-	-	-	-	-	-	-	-
Trichoglossus chlorolepidotus	Scaly-breasted Lorikeet	7	2	2.50	0	-	0	-	0	-
Halcyonidae										
Dacelo novaeguineae	Laughing Kookaburra	2	2	1.00	0	-	0	-	0	-
Halcyon sancta	Sacred Kingfisher	2	1	1.00	0	-	0	-	0	-
Podargidae										
Podargus strigoides	Tawny Frogmouth	2	1	1.00	0	-	0	-	0	-

Family Scientific Name	Common Name	Functional group	Brigalow # Sites (n=20)	Brigalow Average Abund	GrassU # Sites (n=3)	GrassU Average Abund	GrassP # Sites (n=4)	GrassP Average Abund	Cultivation # Sites (n=20)	Cultivation Average Abund
Apodidae										
Hirundapas caudacutas	White-throated Needletail*	-	-	-	-	-	-	-	-	-
Hirundinidae										
Hirundo nigricans	Tree Martin*	-	-	-	-	-	-	-	-	-
Hirundo neoxena	Welcome Swallow*	-	-	-	-	-	-	-	-	-
Maluridae										
Malurus melanocephalus	Red-backed Fairy-wren*	-	-	-	-	-	-	-	-	-
Malurus cyaneus	Superb Fairy-wren	8	4	7.00	0	-	0	-	0	-
Malurus lamberti	Variegated Fairy-wren	8	5	3.80	0	-	0	-	0	-
Pardalotidae										
Pardalotus striatus	Striated Pardalote*	-	-	-	-	-	-	-	-	-
Acanthiza nana	Yellow Thornbill	4	2	4.00	0	-	0	-	0	-
Acanthiza chrysorrhoa	Yellow-rumped Thornbill	1	0	-	1	2.33	0	-	0	-
Meliphagidae										
Lichmera indistincta	Brown Honeyeater*	-	-	-	-	-	-	-	-	-
Philemon corniculatus	Noisy Friarbird	6	1	1.00	0	-	0	-	0	-
Manorina melanocephala	Noisy Miner	6	18	8.61	0	-	0	-	0	-
Grantiella picta	Painted Honeyeater	6	3	1.33	0	-	0	-	0	-
Lichenostomus virescens	Singing Honeyeater	6	2	1.50	0	-	0	-	0	-
Acanthagenys rufogularis	Spiny-cheeked Honeyeater	6	9	2.22	0	-	0	-	0	-
Plectorhyncha lanceolata	Striped Honeyeater	6	16	2.19	0	-	0	-	0	-
Manorina flavigula	Yellow-throated Miner*	-	-	-	-	-	-	-	-	-
Pomatostomidae										
Pomatostomus temporalis	Grey-crowned Babbler	1	6	6.00	0	-	0	-	0	-
Pachycephalidae										
Pachycephala rufiventris	Rufous Whistler*	-	-	-	-	-	-	-	-	-
Dicruridae										
Rhipidura fuliginosa	Grey Fantail*	-	-	-						

			Brigalow		GrassU		GrassP		Cultivation	
Family Scientific Name	Common Name	Functional group	# Sites (n=20)	Average Abund	# Sites (n=3)	Average Abund	# Sites (n=4)	Average Abund	# Sites (n=20)	Average Abund
Myiagra rubecula	Leaden Flycatcher	4	1	1.00						
Grallina cyanoleuca	Magpie-lark	1	12	3.17	1	2.00	0	-	3	0.62
Myiagra inquieta	Restless Flycatcher*	-	-	-	-	-	-	-	-	-
Rhipidura rufifrons	Rufous Fantail	4	3	1.00	0	-	0	-	0	-
Rhipidura leucophrys	Willy Wagtail	1	2	1.50	0	-	1	0.25	0	-
Campephagidae										
Coracina novaehollandiae	Black-faced Cuckoo-shrike	4	7	1.29	0	-	0	-	0	-
Coracina maxima	Ground Cuckoo-shrike*	-	-	-	-	-	-	-	-	-
Lalage tricolour	White-winged Triller	4	2	1.50	0	-	0	-	0	-
Oriolidae										
Shecotheres viridis	Figbird	7	1	5.00	0	-	0	-	0	-
Oriolus sagittatus	Olive-backed Oriole	7	8	1.50	0	-	0	-	0	-
Artamidae										
Gymnorhina tibicen	Australian Magpie	1	12	2.58	3	2.67	2	3.25	11	2.38
Artamus cinereus	Black-faced Woodswallow*	-	-	-	-	-	-	-	-	-
Cracticus torquatus	Grey Butcherbird	1	19	4.74	0	-	0	-	2	0.15
Cracticus nigrogularis	Pied Butcherbird	1	5	1.40	2	1.33	2	1.50	3	0.54
Strepera graculina	Pied Currawong*	-	-	-	-	-	-	-	-	-
Corvidae										
Corvus coronoides	Australian Raven	1	7	2.57	0	-	0	-	1	0.08
Corvus orru	Torresian Crow	1	18	3.67	1	0.33	3	2.25	9	1.31
Corcoracidae										
Struthidea cinerea	Apostlebird	1	13	6.54	0	-	0	-	1	0.46
Corcorax melanorhamphos	White-winged Chough	1	4	4.00	0	-	1	1.00	0	-
Passeridae										
Taeniopygia bichenovii	Double-barred Finch*	-	-	-	-	-	-	-	-	-
Passer domesticus	House Sparrow*	-	-	-	-	-	-	-	-	-
Neochmia modesta	Plum-headed Finch*	-	-	-	-	-	-	-	-	-

Family Scientific Name	Common Name	Functional group	Brigalow		GrassU		GrassP		Cultivation	
			# Sites (n=20)	Average Abund	# Sites (n=3)	Average Abund	# Sites (n=4)	Average Abund	# Sites (n=20)	Average Abund
Taeniopygia guttata	Zebra Finch*	-	-	-	-	-	-	-	-	-
Dicaeidae										
Dicaeum hirundinaceum	Mistletoebird	7	15	2.13	0	-	0	-	0	-
Sturnidae										
Sturnus vulgaris	Common Starling	1	9	3.33	0	-	1	0.50	2	0.31
Sylviidae										
Cinclorhamphus cruralis	Brown Songlark	5	0	-	1	0.33	0	-	1	0.08
Acridotheres tristis	Common Myna	1	12	2.92	1	0.67	1	0.50	3	0.46
Cisticola exilis	Golden-headed Cisticola	5	0	-	0	-	1	0.25	1	0.08
Zosterops lateralis	Silvereye	7	1	2.00	0	-	0	-	0	-
Mirafra javanica	Singing Bushlark	5	0	-	0	-	1	1.50	2	0.38

Appendix 10. Dissimilarity (SIMPER output) between land management for vegetation structural attributes.

Table A10.1. Average dissimilarity between land management categories and the average abundance of vegetation structural attributes that contributed up to 50% of the dissimilarity between land management categories. In each comparison, vegetation structural attributes are listed in decreasing order of their importance in discriminating the two sets of samples.

Species	**Average abundance**		**Cumulative %**
Average dissimilarity = 54.66	**Brigalow**	**Cultivation**	
Bare ground	0.37	0.82	14.93
Shrubs > 2m	0.38	0.00	27.59
Shrubs 1-2m	0.23	0.00	38.10
Trees 10- 20m	0.29	0.00	47.68
Litter	0.59	0.39	56.38
Average dissimilarity = 54.73	**Brigalow**	**GrassU**	**Cumulative %**
Grasses	0.51	0.99	16.57
Shrubs > 2m	0.38	0.00	29.77
Litter	0.59	0.25	41.72
Trees 10-20m	0.29	0.00	51.72
Average dissimilarity = 48.09	**Cultivation**	**GrassU**	**Cumulative%**
Grasses	0.36	0.99	36.08
Bare ground	0.82	0.23	70.06
Average dissimilarity = 51.90	**Brigalow**	**GrassP**	**Cumulative %**
Grasses	0.51	0.92	14.70
Shrubs > 2m	0.38	0.00	28.53
Litter	0.59	0.24	41.21
Trees 10-20m	0.29	0.00	51.68
Average dissimilarity = 41.07	**Cultivation**	**GrassP**	**Cumulative%**
Grasses	0.36	0.92	36.85
Bare ground	0.82	0.37	66.57

Average abundance represents the average cover of structural variables per plot within each land management category. Cumulative % represents the cumulative influence of the variables to the overall Bray-Curtis dissimilarity.