Disturbance and resilience in riparian woodlands on the highly modified Upper Condamine floodplain

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Kathryn Mary Reardon-Smith

BNatRes (Hons), MSc

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ABSTRACT

Remnant ecosystems in agricultural landscapes are poorly understood in terms of their diversity, function and dynamics under altered disturbance regimes, and of how these influence resilience to future disturbance. Understanding native ecosystem responses to novel and multiple disturbances is a crucial foundation for adaptive management to maintain and enhance biodiversity and critical ecosystem services in production landscapes. This is particularly significant where environmental change drives irreversible threshold responses and ecosystem transitions to less functional, or less preferred, alternative ecological states. This research was conducted in remnant riparian woodland ecosystems along a regulated section of the Condamine River, southern Queensland, an ephemeral dryland river system draining an intensively farmed landscape in eastern Australia. Riparian woodland remnants on the Upper Condamine floodplain are subject to significant changes in hydrological regimes and land use intensity. They also exhibit dieback and limited recruitment of canopy species, as well as widespread invasion by the introduced perennial herb *Phyla canescens* (lippia); however, efforts to address these issues have largely failed to curb ongoing degradation, potentially due to a lack of understanding of the key drivers of ecological change operating in this complex socio-ecological landscape.

This research addressed questions about the drivers of floristic composition, functional diversity and woodland condition in fragmented riparian woodland communities associated with a regulated dryland river system, and embedded in a production landscape. In particular, it investigated ecological responses to the range of disturbances (including altered hydrology, land use intensity, resource availability, and key species interactions) prevalent in this highly modified landscape. Two of the four studies presented test the hypothesis that the composition and condition of riparian woodland remnants on the Upper Condamine floodplain are associated with current levels of longitudinal and lateral hydrological connectivity. These studies used a stratified sampling design which partitioned the study area into river sections, and also considered the influence of lateral overbank and overland flood flows, and grazing within ecosystem fragments (remnants). Full floristic sampling and condition assessments of mature *Eucalyptus camaldulensis/E. tereticornis* trees were conducted at a total of 24 sites in 2004/05. Significant patterns in floristic composition, functional diversity and woodland condition were explained by

differences in hydrological variability; however, the confounding influence of land use and interaction between within-remnant land use (specifically grazing) and hydrological factors for some measures, indicated response to a complexity of drivers.

A third study investigated the influence of local and landscape-scale hydrological and land use variables. It used a Bayesian model averaging (BMA) approach to identify informative model sets of explanatory variables, and key environmental predictors of floristic composition, community structure and ecological condition. A novel method was developed to examine dynamic transitions in species richness and abundance between reciprocal pairs of functional groups; this method used the ratio of species richness (or total abundance) in corresponding pairs of functional trait groups (e.g. C3:C4 species) as a community response variable reflecting the relative importance of each group along the environmental gradients tested. Groundwater decline was the primary predictor of ecosystem response, with lower floristic and functional diversity and more severe dieback associated with increasing depth to groundwater; this result suggests an overarching reliance on shallow groundwater resources for maintenance of ecosystem resilience not previously reported for this ecosystem type in Australia. Lippia abundance and dominant tree condition were also important biotic drivers of ecosystem condition in these communities, and key predictors of floristic composition and functional group richness and abundance transitions. Poor tree condition and loss of hydraulic function was associated with secondary impacts on less well adapted ‘terrestrial’ groundcover species, while the subdominant species *Acacia stenophylla* responded positively to competitive release due to poor tree function and reduced tree density. Lippia cover was also strongly associated with the density (positively) and mortality (negatively) of mature trees.

Small scale species interactions were investigated in a study which tested differences in groundcover vegetation composition and lippia cover, reproductive condition and growth habit between ‘distance from tree’ and topographic position treatments in a riparian woodland on the Upper Condamine floodplain. Sampling was conducted along twelve transects extending from the base of mature *Eucalyptus camaldulensis/E. tereticornis* trees into canopy gaps. Results indicated that scattered trees play a significant role in facilitating the abundance and condition of lippia in this landscape, with evidence of high lippia abundance, reproductive effort and

consolidated clonal growth under trees canopies (described as a ‘halo’ effect). This interaction is likely to play a significant role in the persistence of this mesic, though highly adaptive, species in this drought prone landscape. Lippia cover greater than approximately 20% was also found to have a significant impact on the abundance and diversity of non-lippia species in these grassy woodlands.

Results of this research are synthesised in a conceptual resilience-based state and transition ‘riparian woodland response’ model identifying three critical transitions for riparian ecosystem condition and function related to effectively irreversible changes in the landscape: (i) transformation to a lippia-invaded landscape with the introduction, establishment and spread of lippia on the floodplain; (ii) transformation from riparian communities which are well buffered against drought, due to connection with shallow groundwater, to communities reliant on and susceptible to stochastic climatic variability; and (iii) population failure in the dominant functional canopy species complex, *Eucalyptus camaldulensis/E. tereticornis*, and transformation to non-eucalypt-dominant floodplain ecosystem types such as *Acacia stenophylla*-dominant woodlands, floodplain grasslands or lippia-dominant herblands with significantly reduced capacity to provide essential ecosystems services in riparian contexts.

In conclusion, this research indicates that observed condition in riparian woodlands on the Upper Condamine floodplain is an integrated response to a range of disturbances, but that certain changes (in particular, groundwater decline due to overextraction in combination with extended drought) may be critical to the long-term persistence and function of these remnants. This study indicates the importance of systems-based empirical research to developing better understanding of the function and dynamics of remnant ecosystems in highly modified landscapes subject to both natural and anthropogenic disturbance regimes. The resilience-based approach also focuses attention on the key drivers of stability and critical transitions in these complex socio-ecological systems. Such research is vital to evaluating and predicting changes in remnant native ecosystems and the provision of important ecosystem services, and as a basis for adaptive management in multi-use production landscapes.

CERTIFICATION OF DISSERTATION

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

______________________________________ Date: ……/……/… …

Signature of Candidate

ENDORSEMENT

______________________________________ Date: ……/……/… …

Signature of Supervisor (1)

______________________________________ Date: ……/……/… …

Signature of Supervisor (2)

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Chapter 1 General Introduction

1.1 Research overview

Natural systems worldwide are increasingly impacted by human activity (Chapin *et al.* 2006a, Hobbs *et al.* 2006, Safriel 2009), resulting in significant loss of ecological diversity (Laliberte *et al.* 2010). Yet ecosystem diversity (composition and function, *sensu* Noss 1990) is the fundamental basis of landscape function and the provision of ecosystem goods and services that underpin system productivity and human well-being (McCann 2000, Millennium Ecosystem Assessment 2005). The combined effects of anthropogenic pressures, often in combination with natural stressors such as prolonged drought, may drive significant change in terms of composition and function, reducing the capacity of natural systems to respond to disturbances (Folke *et al.* 2004, Hooper *et al.* 2005), and leaving ecosystems prone to ongoing degradation, reinforced by further biodiversity decline (Folke *et al.* 2004, Safriel 2009). They also contribute to secondary impacts in terms of ecosystem service provision, leading to productivity constraints and higher input requirements in production systems (Bell 1999, Laliberte *et al.* 2010), and significant societal costs associated with addressing impacts such as species invasions, loss of landscape function, and declining water quality and availability for downstream water uses (Sinden and Griffith 2007). Understanding the impact of human activity on ecosystems and the consequences of biodiversity change for ecosystem function and service provision is fundamental to ensuring sustainable land management (Lindenmayer *et al.* 2008).

This is especially apparent in floodplain landscapes, which are some of the most highly modified landscapes worldwide (Décamps 1993, Tockner and Stanford 2002). Their low slope, inherent fertility and proximity to water make them a focus for agricultural development, resulting in significant change in land cover and the types and levels of disturbances (Swift 1984, Marston *et al.* 1995). Increasing evidence of declining biodiversity and ecosystem function associated with major land and water use development indicates that ecosystems in highly modified landscapes such as floodplains are at significant risk (Decamps *et al.* 1988, Peterken and Hughes 1995, Kingsford and Thomas 2002). Such landscapes provide an ideal model to investigate the impacts of, and ecological responses to, altered disturbance regimes associated with human activity, and can contribute significantly to our understanding of how ecological systems respond to change. This knowledge is not only vital to our understanding of how management might most effectively respond to limit loss of biodiversity and vital ecosystem services, but also how future disturbances such as climate change might play out across landscapes. There is a significant social imperative to better understand the function and adaptive capacity of such ecosystems in order to minimise degradation and management constraints in high value production landscapes. However, remnant ecosystems in agricultural landscapes in general and floodplain agricultural landscapes in particular are relatively little studied and poorly understood in terms of their diversity, function and dynamics (resilience) under altered disturbance regimes.

This current research investigates the impacts and responses in remnant (*sensu* Saunders *et al.* 1991) floodplain riparian woodland ecosystems in a highly modified, relictual (*sensu* McIntyre and Hobbs 1999) production landscape. This review outlines the theoretical basis for the research, as well as current understanding of floodplain ecology and ecological responses to modified disturbance regimes associated with floodplain development. It concludes with an overview of the studies undertaken in this research, the key questions addressed and the significance of the research in terms of management and restoration of ecosystem function in the model socio-ecological landscape.

1.1.1 Theoretical background

One of the key ecological insights of the 1970s was the recognition of the importance of disturbance and non-equilibrial processes in ecosystems (Huston 1994). This has led to major developments in ecological theory regarding ecosystem change and the regulation of species diversity (i.e. how diversity varies in space and time), and also to a greater understanding of the role of disturbance as a fundamental driver of ecosystem dynamics (Holling 1973, Wu and Louks 1995, Gunderson 2000). It has also led to increasing recognition of the complexity of ecosystem responses and the potential for multiple alternative outcomes or ecosystem states (in terms of composition and function) for a given range of environmental conditions (e.g. Westoby *et al.* 1989, Seastedt and Knapp 1993, Huston 1994, Gillson 2004).

Non-linearities in system response and the possibility of alternative trajectories and ecosystem endpoints challenge the capacity of ecology to predict how systems will respond to new types or levels (intensity, frequency) of disturbance. Yates and Hobbs (1997), Shea and Chesson (2002) and Shea *et al*. (2004) all identify the need for an integrated theoretical framework within which disturbance dynamics can be adequately interpreted and outcomes predicted. Resilience thinking and a conceptual view of ecosystems (particularly socio-ecological systems which incorporate humans as a significant active component) as complex adaptive systems (CAS; Folke *et al.*1996, Levin 1998, Walker *et al.* 2004, Kinzig *et al.* 2006) represent significant progress in this regard. These also provide an overarching framework within which to investigate, interpret and better understand the mechanics of individual systems. Predicting ecosystem outcomes, particularly where there are likely to be non-linear system responses to multiple disturbances, remains a significant challenge (Groffman *et al.* 2006).

Complexity

Ecological systems are inherently complex, comprising large numbers of diverse interacting components which exhibit collective behaviour (patterns and processes) due to emergent properties (Gallagher and Appenzeller 1999) such as self-organisation and adaptation (i.e. system development) in response to environmental change (Holling 1992, Levin 1998, 1999, Wu and Marceau 2002). Self-organization is evident in the hierarchical organization (e.g. trophic webs), spatial and temporal heterogeneity (patch dynamics), connections or flows (interactions, feedbacks) between components, and non-linearities (resilience, threshold behaviour) of ecosystems (Carpenter *et al.* 1999, Levin 1999, Wu and David 2002, Wu and Marceau 2002).

Adaptive capacity describes an ecosystem’s ability to maintain a diversity of components (e.g. species with different traits and presumed ‘function’) (Liebold & Norberg 2004) and critical processes under dynamic environmental conditions (Norberg 2004). It also encompasses the system’s ability to evolve through processes such as the sorting (filtering) and recombination of component species in response to change and altered selection processes (Liebold and Norberg 2004). CAS theory focuses on how community patterns result from the interaction of system components, and how changes in individual components lead to system-level responses and adaptation (Hartvigsen *et al.* 1998, Norberg 2004, Green and Sadedin 2005).

The CAS concept has led to significant development in ecological thinking in relation to landscape ecology and phenomena such as pattern formation and patch dynamics, connectivity and fragmentation, and epidemic processes such as invasion of alien plants (Green 1993, Green and Sadedin 2005). Ecological foundations for the study of complex adaptive systems include an understanding of the role of disturbance in generating heterogeneous patterns within ecosystems (Wu and Loucks 1995), interactions or feedbacks between pattern, process and scale in the landscape context (Wu 1995), and the dynamics of system responses (i.e. stability/resilience, threshold behaviour) (Holling 1973, Gunderson 2000).

Disturbance

Disturbance has been variously defined (e.g. Grime 1979, Huston 1979, 1994, Pickett *et al*. 1989), but includes any discrete event that changes the physical environment or disrupts population, community or ecosystem structure (White and Pickett 1985, Petraitis *et al*. 1989, Laska 2001). Individual disturbance events may have marked effects in terms of biomass removal, and subsequent resource availability and ecosystem productivity (Myster 2001, Yeakley *et al.* 2003, Clarke *et al.* 2005). Disturbance initiates reorganization within ecosystems, frequently exposing new regeneration surfaces, increasing resource availability, and increasing opportunities for the establishment of novel species (Colautti *et al.* 2006, Richardson *et al.* 2007). It also potentially alters species interactions, fundamental processes such as nutrient cycling, successional trajectories and system feedbacks (Bendix and Hupp 2000, Raffa *et al.* 2008).

The history and sequence of disturbance events can significantly influence successional trajectories and ecosystem development (Turner *et al.* 1998), and combinations of different disturbance types, acting at different temporal and spatial scales, can lead to cross-scale interactions and complex ecosystem responses (Holling 1992, Peters *et al.* 2007). Greater levels of uncertainty and variability in successional trajectories are also associated with the occurrence of large infrequent disturbances (Turner *et al.* 1998), as species are unlikely to have evolved adaptive responses to this scale of event. However, long-term dynamics within ecosystems are predominantly influenced by the nature of the prevailing disturbance regime (i.e. the magnitude and timing of historical disturbance events; Hobbs and Huenneke 1992).

Disturbance is a significant driver of diversity (Connell 1978, Huston 1979, 1994) and function in ecosystems (Hobbs and Huenneke 1992), altering the availability of specific resources and the dynamics of interspecific interactions at the local scale (influencing within-patch or *alpha* diversity) (Huston 1979, Hobbs and Huenneke 1992). Variation in disturbance intensity across landscapes contributes to heterogeneous patch conditions and asynchronous community development due to differential responses to the timing and intensity of disturbance events. In this way, disturbance also plays a key role in maintaining diversity at the landscape level (*beta* diversity) by creating a mosaic of patches of different ages and successional stages (Turner 1987, Hobbs and Huenneke 1992, Legendre *et al.* 2005). Succession, in turn, is influenced by differential rates of establishment, maturation and reproduction of species and outcomes of species interactions within patches, as well as biotic exchange (colonisation) between patches (Pickett *et al.* 1987). Current understanding of the importance of disturbance in supporting diverse, well-functioning landscapes is based on the concept of ecosystems as meta-communities which comprise multiple spatially linked (in terms of dispersal) but temporally independent patches (Ward and Stanford 1995b, Gillson 2004).

System response to disturbance can be measured in terms of resilience (i.e. capacity of a system to recover from disturbance and retain its fundamental character in terms of composition and function); resistance (i.e. the level of change in the natural disturbance regime which can be tolerated before significant change in ecosystem composition or function occurs); pattern of response (linear or non-linear); and rate of response (non-linear system responses may show no measurable change until some threshold level is reached, after which a rapid rate of change may occur; response may also occur some time after a disturbance where ecosystems are dominated by long-lived species) (Orwin and Wardel 2004, Orwin *et al.* 2006). A diverse well-functioning system subject to the range and intensity of disturbance historically experienced is expected to exhibit dynamic ‘stability’, indicative of a high level of system resilience (Turner *et al.* 1993, Szabo and Meszena 2007).

Conversely, disturbances which exceed the limits of natural dynamics over time may reduce resilience and increase the potential for unexpected system responses including transition to alternative ecological states with significant changes in community composition or condition indicative of fundamental change in ecosystem function (Cumming and Collier 2005, Briske *et al.* 2008).

Resilience

The concept of ecosystem resilience is fundamental to understanding the nature and dynamics of disturbance-driven systems. Resilient systems can undergo a level of change in response to disturbance, but will recover and retain their fundamental identity (composition, structure and function) through the influence of negative stabilizing feedbacks which confer ‘dynamic stability’ (Suding *et al.* 2004, Briske *et al.* 2006, Suding and Hobbs 2009). Theoretically, a diverse system with high redundancy (functional response diversity *sensu* Walker 1992) will be more resilient to disturbance and exhibit greater dynamic stability than one in which overall and, specifically, functional diversity is limited (Elmqvist *et al.* 2003, Hooper *et al.* 2005). Systems with low diversity, but a high proportion of resistant species, may also exhibit limited response to disturbance, but are likely to exhibit limited functionality (Loreau and Behera 1999, Maestre and Cortina 2004).

Disturbance, which alters underlying abiotic conditions or dominant species interactions and reduces the functional response diversity of a system, may result in loss of resilience (Scheffer *et al.* 2001, Folke *et al.* 2004, van Nes and Scheffer 2007, Hagerthey *et al.* 2008) and increased risk of a ‘switch’ from negative regulatory feedbacks to positive feedbacks which reinforce change (Briske *et al.* 2006, Suding and Hobbs 2009). Change associated with exceeding ecological tipping points (thresholds) is indicated by a fundamental shift in the identity, composition and function of a system, and reorganization into a new stability domain and ‘alternative stable state’ maintained by a new set of negative feedbacks (a ‘regime shift’) (Mayer and Rietkerk 2004, Carpenter and Scheffer 2009). A system which has undergone a regime shift to an alternative stable state is likely also to develop increasing resilience and resistance with time (Laycock 1991, Mayer and Rietkerk 2004, Suding *et al.* 2004), and will generally require management intervention and significant input (energy, investment) to return to its previous (preferred) condition

(Folke *et al.* 2004, Prober *et al.* 2005, Chartier and Rostagno 2006). System recovery may also be unpredictable in a system exhibiting threshold dynamics unless the biotic and/or abiotic changes which induced the threshold response are effectively addressed (Prober *et al.* 2002b, 2005, Hobbs 2007, Suding and Hobbs 2009).

1.1.2 Floodplain landscapes: patterns and processes

Riparian and active floodplain (i.e. parts of the floodplain subject to periodic inundation and progressive drying between flood events) systems are dynamic heterogeneous non-equilibrial adaptive systems, which integrate landscape processes across spatial and temporal scales (Frissell *et al.* 1986, Ward *et al.* 2002, Wiens 2002). The dynamics of riverine landscapes are primarily driven by the action of flowing water (Walker and Thoms 1993, Ward *et al.* 1999, Naiman *et al.* 2005), which drives geomorphic processes such as erosion and sedimentation, channel migration and floodplain formation (Hughes 1997, Ward *et al.* 2002), as well as species dispersal through the movement of plant propagules (Brown 2002, Ward *et al.* 2002) and flood-dependent establishment processes (Mahoney and Rood 1998, Pettit and Froend 2001a,b, Cooper *et al.* 2003a). However, as transitional ecosystems between riverine and terrestrial systems (Thoms 2003), they are also influenced by disturbance within the wider catchment (Tabacchi *et al.* 1998, Thoms *et al.* 1999, Allan *et al.* 2002). In combination, these events contribute to the exchange of materials and energy between riverine and floodplain systems, driving ecological processes, supporting floodplain function, and shaping and sustaining associated ecosystems (Lorenz *et al.* 1997, Gallardo 2003, Naiman *et al.* 2005).

Appreciation of the importance of dynamic processes (e.g. disturbance, recruitment, succession) in terrestrial systems (Wu and Loucks 1995) has contributed to greater understanding of the evolution of complex riverine and floodplain landscapes (Thorp *et al.* 2006), the importance of cross-scale interactions (Thorp *et al.* 2006; Figure 1.1) and mechanisms behind the spatial and temporal heterogeneity evident in dynamic riverine environments (Poole 2002, Thorp *et al.* 2006). Current understanding of the nature and function of active floodplain ecosystems is based on the interactive roles of connectivity and disturbance in driving ecological processes and patterns which shape ecosystem resilience in floodplain landscapes (e.g. Sedell *et al.* 1990, Stromberg *et al.* 1993).

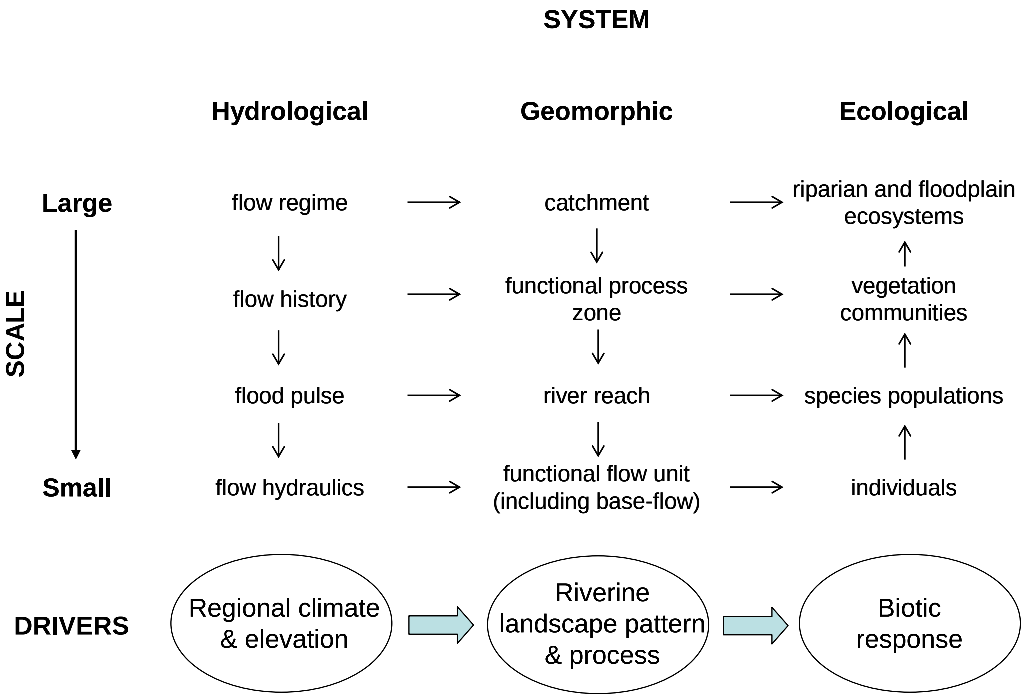


Figure 1.1 Hierarchical relationships between hydrological, geomorphic and ecological systems associated with rivers (adapted from Thoms and Parsons 2002). This conceptual diagram (based on the River Ecosystem Synthesis; Thorp et al. 2006) comprises hydro-geo-ecological hierarchies and cross-scale interactions driving abiotic and biotic processes (including connectivity) and ecological patterns (including heterogeneity) in riverine (riparian and floodplain) landscapes. Arrows indicate potential direction of major flows/influences, but are not exclusive of interactions in any direction, or across/between scales.

Connectivity

Conceptual hypotheses developed to explain geomorphic and ecological processes in river corridors focus on the spatial and temporal nature of hydrological connections. These include the River Continuum concept (Vannote *et al.* 1980), the Flood Pulse (a view of the floodplain as a mobile 'aquatic/terrestrial transition zone'; Junk *et al.* 1989) and Flow Pulse (Tockner *et al.* 2000) concepts, the Hyporheic Corridor concept (the hyporheos being the saturated substrate beneath the stream; Stanford and Ward 1993, Boulton 2007), and the River Ecosystem Synthesis (Thorp *et al.* 2006). Overall, these concepts recognise four key dimensions of hydrological connectivity: longitudinal (upstream-downstream linkages along the river corridor); lateral (transverse linkages across the floodplain associated with overbank flooding); vertical (surface-groundwater linkages within the river corridor); and temporal (the range of timescales relevant to these spatial linkages).

Spatial connectivity plays a critical role in physically linking components across floodplain landscapes. The linear configuration and directional flow of energy and resources highlight the importance of longitudinal and lateral connectivity within the stream corridor (Tabacchi *et al.* 1998, Grant *et al.* 2007), and the ecological consequences of flows and floods are generally well recognised. In-stream flow supports aquatic and semi-aquatic species and ecosystems, and movement (including dispersal) of these within the river corridor (Tabacchi *et al.* 1998, Grant *et al.* 2007, Gurnell *et al.* 2008). Overbank flooding refills floodplain wetlands and promotes increased productivity by supplementing soil moisture and redistributing sediment and plant propagules across the floodplain (Thoms 2003, Leyer 2006, Gurnell *et al.* 2008). The importance of vertical connectivity is also recognised (e.g. Brunke and Gonser 1997, Mackay 2006, Boulton 2007). Exchange between surface and groundwater systems fills shallow alluvial aquifers, access to which is a critical resource for groundwater-dependent (phreatophytic) riparian vegetation (Busch *et al.* 1992, Smith *et al.* 1998, Costelloe *et al.* 2008) and an important buffer to streamflow (as baseflow back to the stream) during extended periods of low rainfall/drought (Dahm *et al.* 2003). Temporal variations in connectivity also play a major role in determining processes which influence the composition, structure and function of riverine (including floodplain) ecosystems (Amoros and Bornette 2002, Thoms *et al.* 2005, Porter *et al.* 2007). Temporal connectivity is often scaled into a hierarchy of hydrological phenomena including the flow regime, flow history, flood pulse, and flow hydraulics (Thoms and Sheldon 2000a,b, 2002, Thoms and Parsons 2003), which are linked to geomorphological and ecological responses (Figure 1.1).

The importance of spatial and temporal connectivity is especially evident in river systems in more arid regions (‘dryland rivers’), where rainfall patterns are variable and erratic and result in ephemeral flows and contrasting states of flood and drought which, in many cases, occur at unpredictable intervals (Sheldon 2005). Ecosystem processes in these naturally highly fragmented (temporally and spatially) river systems may differ significantly from those in perennially flowing river systems, being strongly influenced by wetting and drying cycles (Capon 2003) and by spatial and temporal scales of connectivity (highly variable and often short-lived levels of connectedness during floods, highly disconnected during droughts) between riverine and floodplain components (Sheldon *et al.* 2002, Sheldon and Thoms 2006b). Vertical connectivity between surface waterbodies and shallow alluvial aquifers supports persistence of floodplain waterholes and wetlands during periods of low surface flows (Hatton and Evans 1998, Murray *et al.* 2003, Brunke *et al.* 2003), and may be critical to the health and diversity of riparian ecosystems (Horton *et al.* 2001a, Harner and Stanford 2003, Lamontagne *et al.* 2005a) in these landscapes. Groundwater access may provide a critical temporal buffer for species either directly or indirectly dependent on shallow groundwater systems for survival during periods of extended and severe drought (Elmore *et al.* 2003, 2006a).

Heterogeneity

Variable levels of hydrological connectivity mean that floodplain ecosystems are naturally fragmented along rivers where large-scale dynamic natural processes (e.g. flooding, drought) occur (Ward *et al.* 2001, Thoms *et al.* 2005, Sheldon and Thoms 2006b). Interactions between climate, floods, and plant succession produce variable rates and levels of connectivity and patch turnover (Tockner *et al.* 1998, Whited *et al.* 2007) resulting in significant complexity with different patterns and processes occurring at a range of spatial scales in riverine and floodplain environments (e.g. Huggenberger *et al.* 1998, Thoms *et al.* 2005, 2007). These different landscape legacies (Foster *et al.* 1998, Parsons *et al.* 2006) influence the structure, composition and function of floodplain communities and contribute to high levels of heterogeneity in floodplain ecosystems (Gann *et al.* 2005, Jenkins *et al.* 2005, Jansson *et al.* 2007).

Vegetation patterns in floodplain ecosystems also arise from component species' tolerance and physiological response to disturbance and hydrological conditions such as inundation and waterlogging (Chen *et al.* 2002, Leyer 2005, Capon 2007), wetting-drying cycles, and frequency and timing (seasonality) of flows including floods and no-flow periods (Capon 2003, 2005, Stromberg *et al.* 2006). These phenomena determine the survival, growth, competitive and reproductive fitness of individuals, and act as selective filters on the distribution and abundance of species. Flooding disturbance effectively limits the occurrence of species intolerant of high flow velocities, mobile substrates (scouring, sedimentation) or inundation in these landscapes (Turner *et al.* 2004), while floodplain ecosystems associated with dryland river systems may also exhibit limited diversity of species which are poorly adapted to cope with drought and extreme moisture conditions (e.g. Cleverley *et al.* 1997, Horton and Clark 2001).

Resilience in floodplain ecosystems

Resilience in floodplain ecosystems is fundamentally associated with variability in temporal and spatial connectivity, and the resultant heterogeneity of resources and species distributions across the active floodplain landscape (Tockner 2007). Community assemblages, comprising a diversity of species adapted to the range of conditions associated with the historical disturbance regime, retain the capacity (often through the formation of persistent seedbanks; e.g. Holzel and Otte 2004, Capon and Brock 2006) to respond to this variability, and maintain ecosystem function (e.g. Bagstad *et al.* 2005). For example, Capon (2005) found that frequently flooded sites on the Cooper Creek floodplain, central Australia, were more similar to each other than those which were rarely flooded. Capon and Brock (2006) similarly reported that spatial patterns in soil seed bank composition were associated with the broad flood frequency gradient in this same landscape. Extreme variability (e.g. severe drought) in arid and semi-arid floodplain systems may also be buffered by residual connectivity with shallow alluvial groundwater systems providing critical drought refugia (Sedell *et al.* 1990) which enable species persistence and facilitate the recovery of ecosystem function following drought (Lake 2003).

1.1.3 Floodplain development

By contrast, rivers and floodplains significantly modified by human activities are increasingly disconnected and at odds with their evolutionary dynamics. Anthropogenic changes in landscape configuration (e.g. ecosystem fragmentation), in combination with management intensity, mean that natural disturbance regimes are likely to be significantly altered (Hobbs and Huenneke 1992). Water resource development (flow regulation or extraction) to support and protect irrigated agriculture or urban settlements has led to significant modification of hydrological flow in rivers (Baron *et al.* 2002). Streamflow modification, resulting in altered streamflow and flooding, constrains the exchange of materials (e.g. water, nutrients, sediment) and energy between riverine and floodplain systems which drives natural processes, supports floodplain function, and shapes and sustains associated ecosystems (above). Extraction of water resources to ensure supply to production systems on developed floodplain landscapes results in declining availability to support water-dependent natural systems (Zekster *et al.* 2005, Elmore *et al.* 2006a).

In addition to significant landscape and hydrological change, major land use modification is also almost universally associated with increased presence and diversity of non-native (alien) species (Vitousek *et al.* 1997). These species potentially increase the overall diversity of native ecosystems in these landscapes, particularly where they possess novel traits, occupy alternative niches or contribute to the functional response diversity of what are effectively now novel ecosystems (*sensu* Hobbs *et al.* 2006, 2009). However, where these species are competitive strategists (*sensu* Lambdon *et al.* 2008a), with traits that enable them to access a greater proportion of resources (e.g. Maron and Marler 2008, Schmidt *et al.* 2008) or directly inhibit other species (e.g. Callaway and Ridenour 2004, Vivanco *et al.* 2004), they may become dominant and contribute to declining diversity and heterogeneity within a landscape (Lodge 1993, Lambdon *et al.* 2008a, b). Such species constitute a major disturbance to invaded ecosystems (Mack and D’Antonio 1998, Gooden *et al.* 2009a,b), significantly reducing and displacing native species, altering ecosystem function (Hobbs and Huenneke 1992) and system responses to disturbances (Prober *et al.* 2002b), and modifying subsequent disturbance regimes (the frequency/intensity/type of disturbances) (D’Antonio and Vitousek 1992, Brooks *et al.* 2004).

Highly modified floodplain landscapes and their remnant native (often invaded) ecosystems represent integrated social-ecological systems (*sensu* Carpenter *et al.* 2001), with new or altered drivers of ecosystem structure and function, altered ecological processes and outcomes (Walker and Meyers 2004, Walker *et al.* 2006), and potentially altered resilience (Walker and Salt 2006). In many cases, undesirable changes in composition (with loss of key species and spread of invasives) and a decline in ecosystem function are observed in these landscapes (Fischer and Lindenmayer 2007, Prober and Smith 2009). Despite recognition, the capacity to restore ecological function to developed landscapes is fundamentally constrained by a number of social, ecological and environmental factors. These include the social legitimacy of agricultural land and water use for food and fibre production, the legal property and resource access rights of current landholders, the legacy of historical development (including current extent of biodiversity change and lag effects into the future, and ecological feedbacks to environmental processes and provision of ecosystem services), and lack of understanding of the critical drivers of ecosystem function (Baron *et al.* 2002, Hooper *et al.* 2005).

1.1.4 Disturbance ecology in modified floodplain landscapes

Changes associated with floodplain development have effectively suppressed the range of fluvial dynamics in river systems (Ward and Stanford 1995b), reducing connectivity, limiting the range of natural disturbances and contributing to reduced heterogeneity across floodplain landscapes (Ward *et al.* 1999, Ward and Tockner 2001). This loss of natural environmental dynamism and heterogeneity poses a serious threat to the composition, function and persistence of riverine and floodplain ecosystems (Langhans *et al*. 2006, Stromberg *et al.* 2007a) and may have significant consequences for the continued function of these important socio-ecological systems (Naiman *et al.* 2005). Tockner and Stanford (2002) suggest that up to 90% of floodplains in Europe and North America are essentially functionally extinct as a result of land use change and altered hydrology, with consequent loss of ecological integrity, biodiversity (aquatic and riparian species) and capacity to provide ecosystem services.

'Disconnectivity'

A well-recognised consequence (and threat to biodiversity) of land use change is the incremental fragmentation of native ecosystems, leading to increasingly smaller and more isolated remnant patches within a relatively inhospitable matrix (Cox *et al*. 2001) and significant secondary impacts on biodiversity (McAlpine *et al.* 2002). Patch size and connectedness (proximity to similar patches) are important factors for the persistence of many species within agricultural landscapes (Dale *et al.* 2000, Prober and Smith 2009), influencing the extent of available habitat and dispersal of native species (e.g. Cale 2003). However, it is not clear that this hypothesis is directly applicable to dynamic disturbance-driven riparian ecosystems (Holl and Crone 2004, Wimberly 2006), or to plant species whose dispersal is facilitated by the directional movement of water (Tabacchi *et al.* 1998, Jensen *et al.* 2008a, b).

Fragmentation of riparian ecosystems may be more strongly associated with the presence of in-stream and floodplain structures, such as dams, weirs and levees, which constrain flow, disrupt dispersal pathways and natural disturbance regimes, shorten environmental gradients and upstream-downstream linkages, and isolate river channels from riparian and floodplain systems (Ward 1998, Andersson *et al.* 2000, Jansson *et al.* 2000 a,b). These alterations interfere with successional trajectories, habitat diversification, migratory pathways and other processes associated with connectivity within riverine and floodplain systems (Ward 1998). The term ‘serial discontinuity’ (Ward and Stanford 1993, 1995a), was coined to describe the disruption of riverine biotic and abiotic processes as a consequence of dam and weir construction along the river continuum. However, this was based on an understanding of unregulated rivers as single-thread continually flowing systems (Ward and Stanford 1995a), and fails to account for the variability inherent in many systems (Ward *et al*. 2002). In reality, flow regulation may have disparate impacts, depending on the nature of the stream and the attribute of interest (Nagler *et al.* 2007). In ephemeral streams which undergo periodic fragmentation due to highly variable precipitation and flow conditions, smaller regulatory structures such as weirs may have limited adverse impact, and in fact may act to enhance the frequency of in-stream drought refugia (Sedell *et al.* 1990, Lake 2000) and the extent of surface-groundwater exchange (shallow groundwater aquifer recharge) (Lane and Zinn 1980).

Of greater significance to riparian ecosystems, particularly in dryland river systems, is flow regulation and management for flood mitigation or water supply purposes which significantly alter the frequency and seasonality of flows and reduce the inherent temporal variability of in-stream flow patterns (Ward and Stanford 1995b). In terms of spatial connectivity, flow regulation moderates flood peaks and the frequency, extent and duration of over-bank flooding, and hence, the extent of lateral connectivity across the floodplain (Ward and Stanford 1995b, Ward *et al.* 1999).

Failure to reconnect and rejuvenate floodplain wetlands, for example, limits dispersal and recruitment of flood- and wetland-dependent vegetation species and enables ecological succession to proceed, leading to increasing terrestrialisation (*sensu* Ward *et al.* 2001) and replacement with flood-intolerant habitat-generalist species (Marston *et al.* 1995). This may eventually result in loss of wetland ecosystems (Ward *et al.* 1999, Deil 2005) and functional diversity (specifically, species adapted to flooding) across the landscape (Capon 2007). Floodplain riparian forest structure may also be significantly impacted by altered flows which mimic drought conditions and restrict successful recruitment of ecosystem dominants, such as *Populus* and *Salix* in regulated sections of the upper Colorado basin, USA (e.g. Cooper *et al.* 2003b).

Water extraction (for urban, mining or agricultural purposes) can also have a major impact on in-stream flow volumes, particularly in dryland river systems subject to variable precipitation and flow (Pringle 2000, CSIRO 2008). This is further complicated where flows are diverted and distributed away from the main river channel, and where groundwater pumping from the shallow alluvial aquifer contributes to dewatering of river reaches (Zekster *et al.* 2005, Evans 2007, CSIRO 2008). Increasing discontinuity (intermittency of flow) in ephemeral streams and declining groundwater levels, associated with prolonged drought or dewatering of groundwater aquifers through extraction, can lead to disconnection between surface and underground waterbodies (Braaten and Gates 2003, Evans 2007, CSIRO 2008). This disconnectivity has potentially important consequences for phreatic (groundwater-dependent) species and ecological systems, exacerbating drought conditions and leading to decline in individual species and loss of functional diversity across affected landscapes (Stromberg *et al.* 1996, Elmore *et al.* 2003). Riparian species have been referred to as ‘drought avoiders’ due to their reliance on ready access to water (usually subsurface/groundwater) (Smith *et al.* 1998). They are frequently physiologically adapted to and dependent on high water availability, lack the physiological capacity to reduce water use, and risk significant physiological constraints due to hydraulic failure under low water conditions (Alder *et al.* 1996, Pockman and Sperry 2000, Rood *et al.* 2000). Decline in groundwater levels or reduced flooding can contribute to increased mortality in such species (e.g. Akeroyd *et al.* 1998, Lytle and Merritt 2004, Horner *et al.* 2009).

Homogeneity

Altered biodiversity patterns at a range of scales (e.g. reduced landscape diversity, ecosystem homogenisation, changes in species composition and population fitness) are universally reported where floodplain landscapes are subject to land use development and modified hydrological regimes (e.g. Rood and Mahoney 1990, Stromberg *et al.* 2005a, Dufour *et al.* 2007). Reduced frequency, extent and duration of flooding limit the lateral connectivity of the floodplain, its water bodies and vegetation communities with the main river channel. Fluvial processes and associated channel migration, erosion and sedimentation, become less dynamic (Shields *et al.* 2000), and dispersal of floodplain organisms or their propagules is suppressed (Beauchamp and Stromberg 2008, Middelton and Wu 2008), as is reproduction and recruitment in species responsive to flooding (Horton and Clark 2001, Stromberg *et al.* 2007a).

Comparisons between regulated and unregulated river systems show evidence of loss of heterogeneity at a range of temporal and spatial scales with reduced inundation and connectivity across the floodplain (Bowen *et al.* 2003). This includes a range of impacts, from reduced variation in patch distribution across the floodplain landscape (Ward and Stanford 1995b, Stromberg *et al.* 2007a) to changes in nutrient cycling and ecological processes associated with a moving littoral zone (Bowen *et al.* 2003). Lack of flooding and increasing isolation of the floodplain from the river removes an important environmental selection filter which maintains flood-dependent species and constrains the more terrestrial or flood-intolerant species, leading to increasing terrestrialisation and reduced functional diversity of vegetation patches across previously active floodplains (Ward *et al.* 2001, Petrone *et al.* 2005).

In combination, flow modification and geomorphic changes associated with reduced flooding result in a more homogeneous landscape, with overall loss of patch diversity and simplification of within-patch structure (Stromberg *et al.* 2005a) (i.e. reduced *beta*-diversity). Changes in species composition and declining species richness in response to reduced temporal and spatial heterogeneity associated with reduced disturbance and reduced resource availability contribute further to ecosystem homogenisation (Stromberg *et al.* 2005a) (i.e. reduced *alpha*-diversity). Reduced flooding, dewatering of rivers and associated aquifers, especially in combination with periodic drought, drive floodplain landscape drying ('desertification') and may induce compositional shifts toward drought-tolerant species (e.g. Stromberg *et al.* 1996, 2005a).

These processes are also evident in dryland ephemeral river systems; flow regulation and abstraction contribute to significant flood modification and dewatering of the river system, its alluvial aquifer and potentially the floodplain landscape. However, the presence of in-stream regulatory structures such as weirs may act to counter the trend towards overall homogeneity and biodiversity decline to some extent, providing critical drought refugia which enable some species to persist (e.g. Sedell *et al.* 1990, Jacobsen and Kleynhans 1993, Kinzli and Myrick 2009), and supplementing alluvial aquifers through groundwater recharge (Lane and Zinn 1980).

Resilience in modified floodplain ecosystems

Altered hydrological pattern is a significant driver of change in riverine and riparian ecosystems, contributing to decline in dominant tree species (e.g. Rood and Mahoney 1990, Lytle and Merritt 2004, Stromberg *et al.* 2007a), increased opportunity for invasion by alien species (e.g. Stromberg *et al.* 2007b) and potentially a shift in community structure (Capon 2003), although few studies have investigated this. Stromberg *et al.* (2007a) report reduced diversity and cover of herbaceous (and particularly perennial) species at local scales and reduced landscape patch heterogeneity, where river regulation and water diversion resulted in increasing intermittency of in-stream flows, associated groundwater decline and replacement of dominant canopy species by more drought-tolerant and less groundwater-dependent canopy species. Altered sedimentation rates and coarsening of substrates downstream of reservoirs in this study also reduced the water- and nutrient-holding capacity of soils, contributing further to altered cover and richness of herbaceous vegetation (Stromberg *et al.* 2007a). Elmore *et al.* (2003, 2006a) report a shift in species composition in alkali meadows from perennial to alien annual herbaceous species where groundwater declined below the average rooting depth of 2.5 m, resulting in the decoupling of vegetation cover from shallow groundwater, which provided a buffer during drought, and a functional shift to increased response to precipitation. The study showed a slower rate of change where deep-rooted woody (shrub) species were present suggesting that these moderated the effect of groundwater decline to some extent (Elmore *et al.* 2006a).

Altered hydrological regimes are also reported to facilitate the dominance of invasive alien species which further contribute to the altered composition, structure and function of remnant ecosystems in these landscapes. Flow regulation and the subsequent dampening of the hydrological variability of streams in the arid south-western USA have contributed to decline in the native dominant canopy species, *Populus* spp. and *Salix* spp., and increased prevalence of the more drought-tolerant alien invasive species, *Tamarix ramosissima* (Stromberg 1998a,b, Stromberg *et al.* 2007b). However, the potential impact of such species on community structure and resilience in riparian ecosystems has received limited attention. In South Africa, restoration of alien-invaded riparian zones relies on regeneration of native species from the persistent soil seedbank after clearing of alien tree species such as *Acacia longifolia*; however, not all riparian species are represented in the soil seedbank (Vosse *et al.* 2008), indicating a potential impact on functional response diversity in invaded communities.

1.1.5 Key knowledge gaps

Increasing awareness of the importance of ecosystem services, in conjunction with evidence of significant decline in native ecosystems in highly modified landscapes, has led to an increased focus on understanding the response (i.e. resilience, stability, threshold behaviour) of these systems to anthropogenic change (Walker *et al.* 2002, Carpenter *et al.* 2006, Laliberte *et al.* 2010). However, despite considerable development in the theories of resilience and complex adaptive systems (Hobbs and Suding 2009), there has been limited empirical research reported to date. Research to identify alternative states and potential thresholds in managed ecosystems (predominantly in grazed rangelands) has also incorporated key elements of resilience thinking (Briske *et al.* 2006, 2008). However, terrestrial ecological systems research has largely focused on compositional and functional responses to grazing disturbances, predominantly in semi-natural grazed rangelands (e.g. McIntyre *et al.* 1995, Lavorel *et al.* 1999a, Diaz *et al.* 2007). Few studies have been conducted in highly modified landscapes where multiple, potentially interacting disturbances are at play, with the exception of work on resilience in socio-ecological systems (*sensu* Holling 2001) (Walker *et al.* 2002, 2004, Folke 2006, Kinzig *et al.* 2006). As a result, there is limited understanding of the resilience of natural systems to the cumulative impacts of multiple disturbance gradients.

Studies into the ecology of remnant ecosystems in modified landscapes have focused on the geometry of landscapes (patch size, shape and separation) (Forman 1995) and, to a lesser extent, impacts associated with the nature of the surrounding agricultural matrix (e.g. Collard 2007, Martin *et al.* 2006). The majority of such studies have focused on individual (or select groups of) faunal species (e.g. Martin *et al.* 2006, Kath *et al.* 2009, Brady 2010), although Batterham (2008) investigated the effect of patch geometry on tree health and population processes in the dominant floodplain canopy species *Eucalyptus populnea*. Declining health of canopy species in response to land use intensification has also been investigated in a number of instances (e.g. Jones *et al.* 1990, Wylie *et al.* 1992, 1993, Davidson *et al.* 2007, Banks 2006). However, there has been little focus on understanding the effect of surrounding land use on the overall condition, composition or function of remnant ecosystems in these landscapes (Kleyer *et al.* 2007), and few, if any, studies looking at impacts on riparian communities.

Research in riparian communities has focused on the impacts of river regulation and altered flow regimes on diversity, health and population processes in dominant riparian canopy tree species (e.g. Shafroth *et al.* 2002a,b, Cooper *et al.* 2003a, Lambs *et al.* 2006). While these species are possibly keystone species (Mills *et al.* 1993, Manning *et al.* 2006) in these environments and often important in terms of ecosystem function (Stromberg *et al.* 1996, Sabater *et al.* 2000), the flow-on effects of changes in dominant structural species on community structure and resilience has received limited attention. Widespread recognition that floodplain riparian systems are disturbance-driven ecosystems, and of considerable importance in terms of ecological function and environmental service provision (Tockner and Stanford 2002, Sweeney *et al.* 2004), indicates a need for a systems-based understanding. The time-lag involved in measurable response in relatively long-lived and adaptive species such as canopy tree species (e.g. Chapin *et al.* 1993, Kozlowski and Pallardy 2002) further reinforces the potential risk associated with an approach which uses these as indicators of system response, increasing the risk that critical ecological thresholds may be exceeded before the need for management response is apparent (Eamus *et al.* 2006, Michelson 2008).

A limited number of studies have investigated changes in the composition, structure and function of these systems in response to altered hydrology (e.g. Leyer 2004, 2005, Sluis and Tandarich 2004, Stromberg *et al.* 2005a, 2007b, Uowolo *et al.* 2005), and some have identified hydrological thresholds associated with alternative ecosystem states (e.g. Leyer 2004, Stromberg *et al.* 2005a). No such studies appear to have been conducted in Australia, where the focus has been on riparian and floodplain canopy tree health and population processes in response to altered flooding regimes (e.g. Pettit and Froend 2001b, Robertson *et al.* 2001), landscape hydrology and salinisation (e.g. Jolly *et al.* 1993, 1996, Overton *et al.* 2006).

Despite limited ecological understanding, there is considerable evidence that changes to hydrological regimes, as a result of flow modification and associated water resource development, are having significant ecological impact in riverine and riparian environments, including adverse impacts on population processes in a number of water-dependent species groups (e.g. waterbirds, fish, riparian tree species) (Kingsford 2000, Bunn and Arthington 2002). Within the last decade in Australia, there have been increasing moves to address this through the provision of environmental flows designed to meet the requirements of identified ‘environmental assets’ such as iconic species (e.g. Murray river cod *Maccullochella peelii peelii* and river red gum *Eucalyptus camaldulensis*) and high priority wetlands (e.g. the Barmah-Millewa Forest, Chowilla Floodplain, the Lower Murray lakes) (Reid and Brooks 2000, Stewart and Harper 2002). Within the Murray-Darling Basin, in which hydrological regimes are highly modified and water resources are significantly over-allocated (Kingsford 2000, CSIRO 2008), this process faces significant social and legal (policy) hurdles associated with the current level of development (Ladson and Finlayson 2002). Lack of scientific ‘certainty’ is a significant factor in the public debate (White *et al.* 2010), and frequently acts to undermine both political will and ultimately the capacity for change. Variation in over-arching climatic systems across Australia also signifies the need for better understanding of the particular dynamics of individual systems, and the incorporation of these into planning and management, and increased adherence to and application of the ‘precautionary principle’ in natural resource management policy (COMEST 2005).

1.2 Aims and scope of current study

The review of literature presented above indicates a growing understanding of the role of disturbance, and in particular the hydrological regime, as a key driver of ecological patterns and dynamics in floodplain and riparian ecosysytems. However, it also indicates the importance of better understanding how these factors operate in conjunction with changes associated with anthropogenic modification in socio-ecological landscapes where ecosystem values, including the provision of ecosystem services, are significantly altered. This research seeks to address the fundamental need for hypothesis-driven systems-based empirical research to document, understand and predict native ecosystem responses and the socio-ecological consequences of altered hydrological regimes and land use change, to aid informed land and water management decision-making aimed at optimizing social, economic and ecological outcomes within ‘working’ landscapes such as the Upper Condamine Floodplain.

1.2.1 Research questions

This study examines the relationship between major landscape (land cover, land use) and hydrological change and the resilience of remnant native floodplain ecosystems embedded in a production landscape in southern Queensland. It investigates ecosystem responses to landscape modification and current disturbance regimes in riparian vegetation communities associated with the regulated section of the Condamine river system in an intensively farmed area of the Upper Condamine floodplain. It identifies major land and water use gradients associated with patterns in floristic composition and ecosystem condition in this landscape. It also investigates finer-scale interactions between community composition and key species which play a critical functional role in these communities.

Specific questions addressed include:

(i) are patterns in floristic composition and ecological condition in riparian woodland remnants associated with current levels of longitudinal, lateral, vertical and temporal hydrological connectivity on the Upper Condamine floodplain;

(ii) is the hydrological regime the dominant driver of floristic composition, community structure and ecological condition in remnant riparian woodland communities within the highly modified production landscape of the Upper Condamine floodplain;

(iii) what are the key environmental gradients driving community dynamics as evident in measures of floristic composition, community structure and dominant species condition in remnant riparian woodland communities on the Upper Condamine floodplain;

(iv) do interactions between key species (dominant canopy species, dominant invasive weed species) play a significant role in determining floristic composition and ecological condition in these communities; and

(v) what are the implications of significant landscape modification for continued ecological function, including resilience, in riparian woodland remnants on the Upper Condamine floodplain?

1.2.2 Thesis outline

A detailed overview of the study area is provided in Chapter 2, which describes the biophysical characteristics and major environmental changes associated with land and water use development on the Upper Condamine Floodplain. In particular, this chapter documents patterns in streamflow and land use type and intensity at the river section and river bank scales by which the riparian landscape is stratified in studies reported in Chapters 3 and 4.

Chapters 3 and 4 present the results of a survey of *Eucalyptus camaldulensis/E. tereticornis* riparian woodlands and their composition and condition in relation to broad hydrological, spatial and land use criteria on the Upper Condamine floodplain. Chapter 3 focuses on major patterns in species composition, particularly in functional trait groups identified as relevant to the dominant disturbance regimes in this landscape. Chapter 4 is concerned with patterns in the abundance and condition of dominant canopy species. These studies test the hypothesis that longitudinal and lateral hydrological connectivity are key drivers of ecosystem pattern in riparian woodland remnants in this landscape (hence relate to Question1, above). They also test the role of within-remnant land use (i.e. grazing), which is reported to interact with hydrological disturbance to influence community composition and structure in riparian landscapes (e.g. Sharp and Whittaker 2003, Lunt *et al.* 2007a, b).

The study reported in Chapter 5 tests the over-riding importance of the hydrological regime in determining community patterns in remnant riparian woodland embedded in highly modified Upper Condamine floodplain landscape (i.e. Question 2, above) by modeling key community responses to sets of environmental variables which capture hydrological and spatial (land use/land cover) attributes at local landscape scales from within-patch to a multi-patch scale. This chapter also identifies key predictors ('drivers') in these woodland response models (i.e, Question 3, above). Potential drivers include environmental variables which capture gradients in levels of disturbance, connectivity, land use intensity and resource availability, as well as the abundance and condition of dominant species (*Eucalyptus camaldulensis/E. tereticornis* and the invasive alien herb *Phyla canescens*) in these communities. Modelled community responses include multivariate floristic composition, gradients in community structure based on a newly developed dynamic measure of functional diversity transitions between reciprocal pairs of functional groups, and patterns in dominant species attributes.

Chapter 6 presents the results of a study investigating the role of local-scale species interactions (facilitation and competition) in these woodlands (i.e. Question 4, above). This study tests the influence of trees on resource availability and groundcover composition, with a focus on the invasive perennial species *Phyla canescens* as an indicator and possible driver of ecosystem change within a riparian woodland remnant on the Upper Condamine floodplain.

In Chapter 7, the results of these studies are synthesised and incorporated into a conceptual 'state and transition' model which identifies alternative ecosystem states and critical transitions apparent in these riparian woodland remnants within the broad context of the Upper Condamine production landscape (i.e. Question 5, above). Research limitations are discussed, and knowledge gaps and future research priorities are identified.

Chapter 8 presents the general conclusions from this research and discusses the potential implications (and limitations) for management aimed at supporting ecological function in remnant riparian woodlands on the Upper Condamine floodplain. It also discusses the relevance of these findings to the broader context of management to retain well-functioning native ecosystems, and in particular water-dependent ecosystems, in highly modified production landscapes.

Chapter 2 Hydrological and land use changes on the Upper Condamine floodplain

2.1 The Upper Condamine floodplain

Located in inland southern Queensland, Australia, the Condamine-Balonne River is a major headwater of the Murray-Darling, Australia's largest river system (Figure 2.1). The Condamine section of the river rises on the western slopes of the Great Dividing Range and flows inland in a broad north-western arc (Figure 2.1). Approximately 250 km from its source, it joins Dogwood Creek, where it becomes the Balonne River, and flows south into New South Wales to then become the Darling.

The Condamine catchment comprises an area of 29,150 km^2 (McKay *et al.* 1999). Approximately 30% (8,500 km^2) of this is alluvial floodplain (Knowles-Jackson and McLatchey 2002), identified regionally as the Upper Condamine, Jimbour and Brigalow floodplains (Figure 2.1). The area of the Upper Condamine Floodplain (between Warwick and Macalister, north-west of Dalby) is approximately 5,000 km^2 and encompasses the main branch of the Condamine River, the Condamine North Branch, and the lower sections of a number of tributary streams (Figure 2.1).

2.1.1 Geology and Soils

The Upper Condamine floodplain comprises predominantly basalt-derived alluvial sediments consisting of heterogeneous deposits of sandy-silty clays up to 134 m thick (Huxley 1982, Kelly and Merrick 2007). These extend from the main river channel and its tributaries to the valley margins, where they are bordered by a broad elevated volcanic plateau to the east, and by low sedimentary and igneous hills to the south and west (Huxley 1982).

Major soil types on the floodplain are cracking clays, classed as Vertisols (Isbell 1996) or Black Earths (Great Soil Groups Ug5.15 and 5.16; Dalgleish 1998), with characteristic high fertility, high surface pH (>7) and high moisture-holding capacity (Dalgleish 1998, Douglas *et al.* 1999).

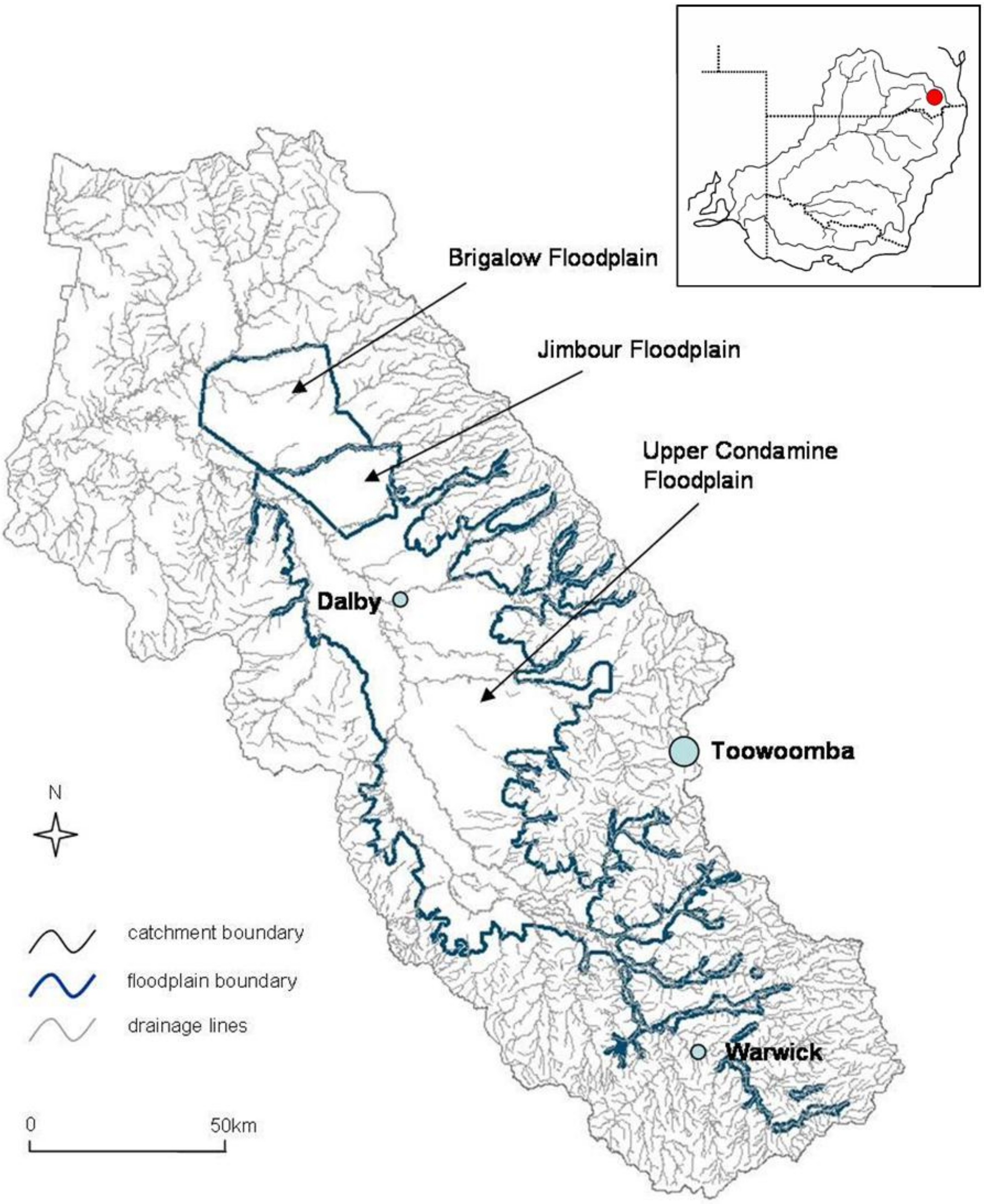


Figure 2.1 Map of the Condamine catchment, showing the location of the Upper Condamine and adjacent floodplains, major towns and drainage patterns. Inset indicates the catchment position at the head of the Murray Darling Basin.

2.1.2 Climate

The climate of the region is classed as an E4 agro-climate (Hutchinson *et al.* 1992, 2005), characterised as warm and seasonally wet or dry, with long hot summers, mild winters and plant growth limited by moisture rather than temperature. Average temperatures at Dalby (Dalby Post Office, 1893–1992) range from 11.9°C to 26.2°C (BoM 2010), although frost and heat wave conditions are frequently experienced (Douglas *et al.* 1999). Average rainfall is summer-dominant (Figure 2.2), but significant rainfall events can occur at any time of the year. Rainfall patterns vary spatially across the catchment along an east-west gradient (Thoms and Parsons 2003), with average annual rainfall of 944 mm.year^{-1} in Toowoomba (Toowoomba, 1869–2007; BoM 2010) and 676 mm.year^{-1} in Dalby (Dalby Post Office, 1870–1992; BoM 2010).

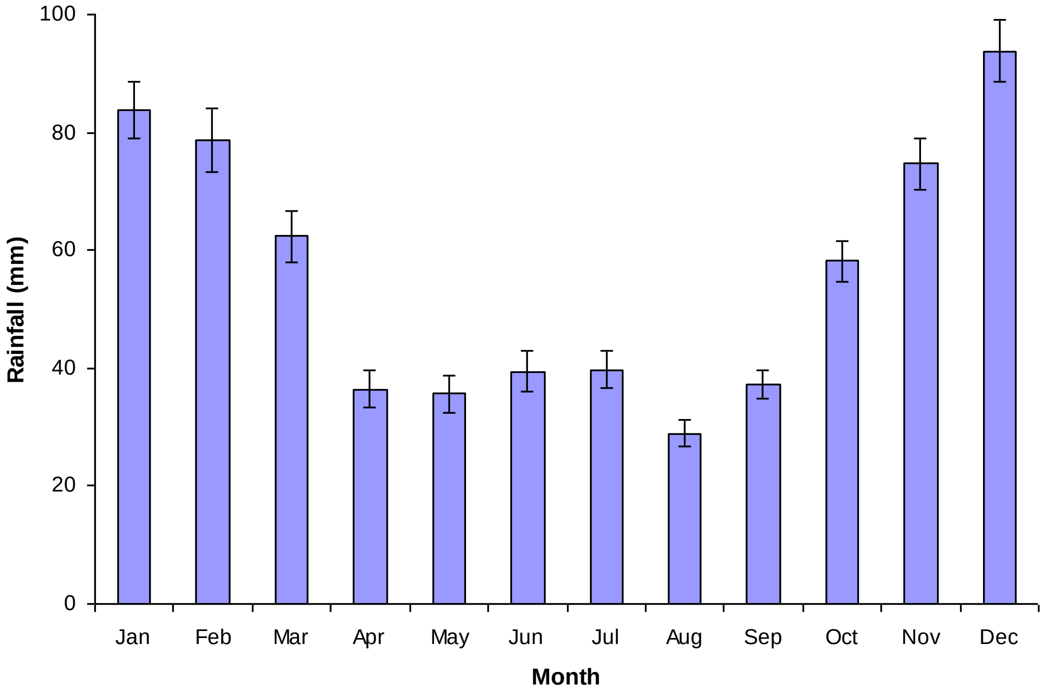


Figure 2.2 Mean monthly rainfall at Dalby (Dalby Airport Composite, 1870–2005; Clewett *et al.* 2003). Error bars are standard error.

Inter-annual variability is high, with annual rainfall at Dalby ranging from 268 mm to 1,273 mm over the recorded period (1870–2010) (BoM 2010). Significant supra-decadal wetting and drying trends are also evident when the cumulative difference between annual and average rainfall is plotted using the cumulative rainfall departure method (Xu and van Tonder 2001, Weber and Stewart 2004) to provide a general indication of rainfall trends over the recorded period (e.g. Tilahun 2006) (Figure 2.3). The drying trend apparent since the 1990s (Figure 2.3) is in agreement with recent rainfall patterns (1997 to 2006), when average annual rainfall and runoff were 2% and 23% lower, respectively, than longterm (1895–2006) averages (CSIRO 2008).

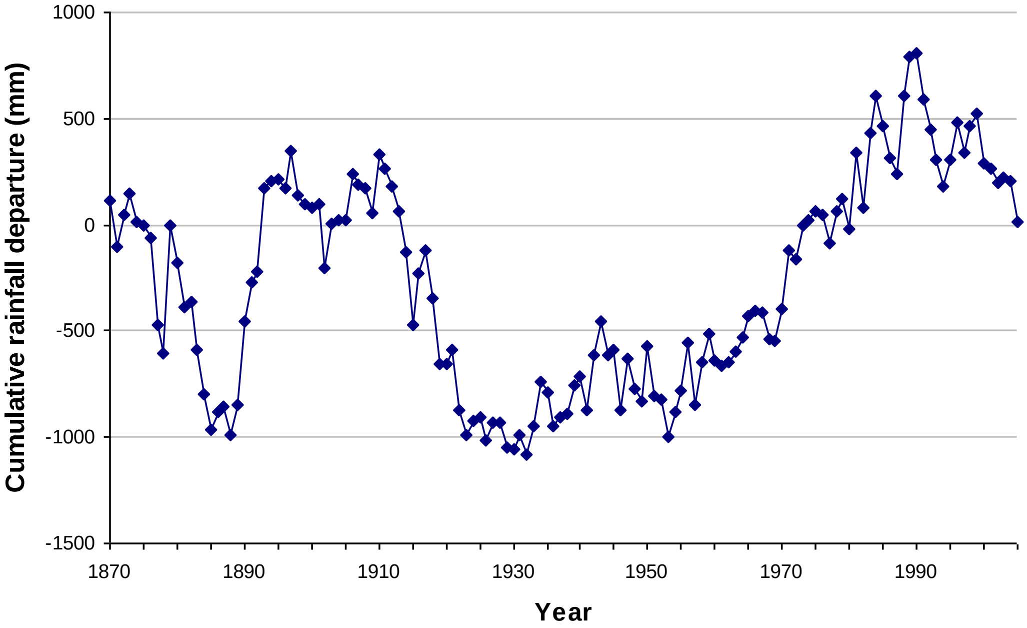


Figure 2.3 Cumulative rainfall departure patterns indicate major wetting (positive slope) and drying (negative slope) trends evident in annual rainfall from 1870 to 1999 at Dalby (Dalby Airport Composite; Clewett *et al*. 2003).

Drought is a common feature in the climate record of the region. Douglas *et al*. (1999) report 21 moderate to severe droughts at Dalby in the 126 years of rainfall records to 1999. These are defined as periods of 12 or more months' duration which receive less rainfall than the driest 10% (moderate) and 5% (severe) of calendar years at that location. The average duration of droughts recorded is 20 months (Dougls *et al.* 1999), and the longest duration drought on record was from August 1990 to November 1993 (40 months, of which ten months was 'severe') (Douglas *et al.* 1999, BoM 2010). In the decade since 1999, there have been three significant drought periods of 21, 15 and 24 months' duration, the most severe being from March 2004 to May 2005, with 75% of this period in severe drought (BoM 2010).

2.1.3 Hydrology

As with rainfall, average streamflow in the Condamine is summer-dominant (Figure 2.4), but highly variable and essentially ephemeral, with periods of no-flow and occasional large over-bank flood events (Sheldon *et al.* 2000). Annual (water year) streamflow recorded at Cecil Plains Weir (the site of the longest running streamflow records) averaged 347.7 ± 57.5 $GL.year^{-1}$ between October 1947 and September 2005, but ranged from 0.3 $GL.year^{-1}$ (2004/05 water year) to 1,695.9 $GL.year^{-1}$ (1987/88) (Figure 2.5). Over the period to 1999, localised flooding at Cecil Plains occurred on average every 1.1 years and major flooding (defined as gauged river heights of ≥ 8 m at Cecil Plains Weir) every 5.1 years (Douglas *et al.* 1999).

Streamflow and flood events are naturally major sources of groundwater recharge to alluvial aquifers associated with the river (Kelly and Merrick 2007). Some contributions also derive from the upland basalt and sedimentary rock areas on the valley sides, but rainfall infiltration across the floodplain is thought to comprise a relatively small component (Kelly and Merrick 2007) due to the heavy clay soil types (Huxley 1982). Despite this, deep drainage under irrigated crops may be locally significant (Silburn *et al.* 2004, Kelly and Merrick 2007, Silburn and Montgomery 2008).

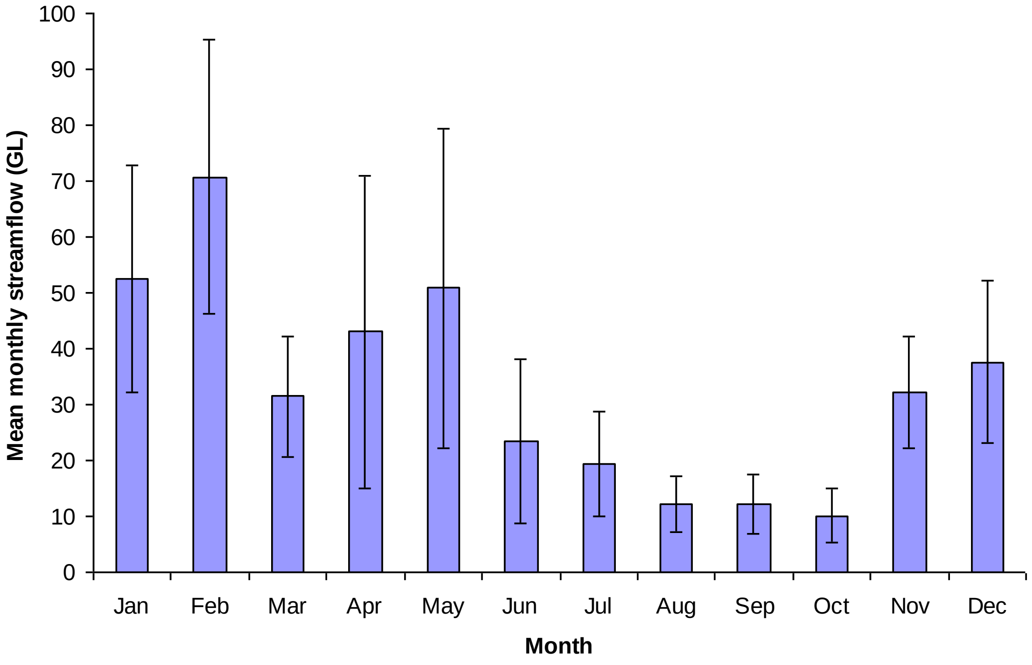


Figure 2.4 Mean monthly streamflow at Loudon Weir, Dalby (1970–1999; Clewett *et al.* 2003). Error bars are standard error.

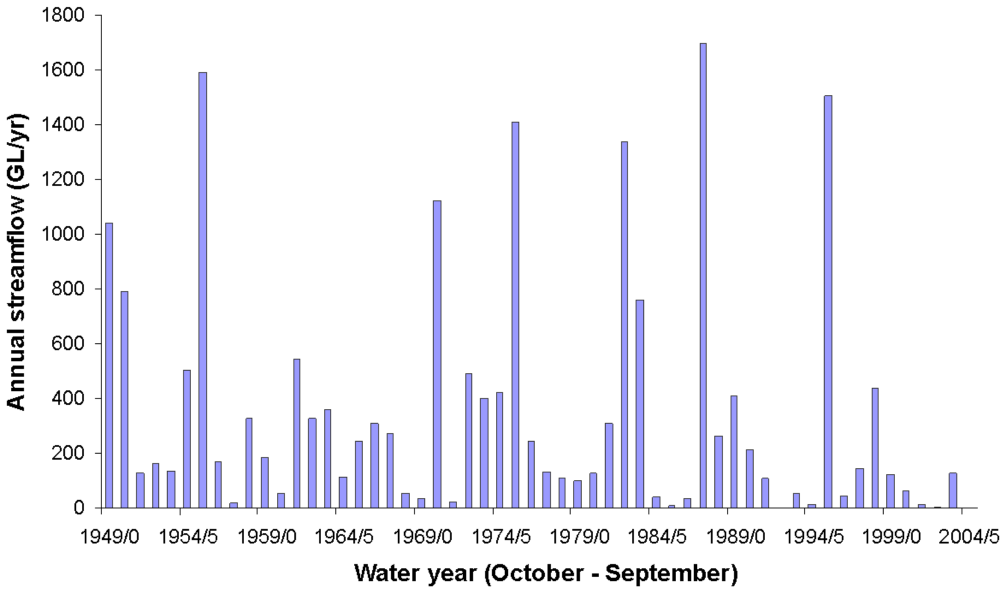


Figure 2.5 Annual streamflow at Cecil Plains Weir, 1949/50–2004/05 (Streamflow records, Streamgauge #422316a, DERM 2010b).

2.2 Development on the Upper Condamine floodplain

2.2.1 Land use development on the Upper Condamine floodplain

Extensive agricultural development on the Upper Condamine floodplain has occurred as a consequence of its deep fertile soils and relatively mild climate, supplemented by significant development of surface and underground water resources (McKay *et al.* 1999). First described by Alan Cunningham in 1827 as "*open plains or downs of great extent*" (Favenc 1908, cited in Scott 2005), the area was initially settled in 1840 when sheep were first brought across the Condamine from NSW (French 1989, cited in Fensham and Fairfax 1997). Large scale pastoral enterprises dominated until the early 1900s when land subdivisions, as well as improved transportation and refrigeration, saw the rise of dairying (French 1994). By 1937, there were more than 6,500 dairy farms on the Darling Downs (Biggs and Carey 2006).

The first recorded cropping on the Downs was near Warwick in 1843. By 1887, some 20,000 hectares, mostly of sloping, better-drained land, were under cultivation (Carberry 1995, cited in McCosker 1996). The first tractor reported on the Downs was in 1912, and the first successful wheat harvest on the black soil plains was in 1931 (Queensland Newspapers 2001). Technological advances in large-scale farming equipment capable of cultivating heavy clay soils led to a rapid transition (post World War II) to cropping on the floodplain. By the late 1950s, most of the lower slopes and floodplains were under cultivation (Carberry 1995, cited in McCosker 1996).

The development and intensification of both dryland and irrigated cropping has continued over the past 50 years or so. The floodplains of the Condamine catchment (part of the Darling Downs) are currently some of the most productive agricultural lands in Australia (Biggs and Carey 2006, CSIRO 2008). Current land use on the Upper Condamine floodplain is dominated by cropping (dryland and irrigated) (Figure 2.6), with a range of winter and summer crops grown including cereals, pulses, maize, sorghum and cotton (Biggs and Carey 2006).

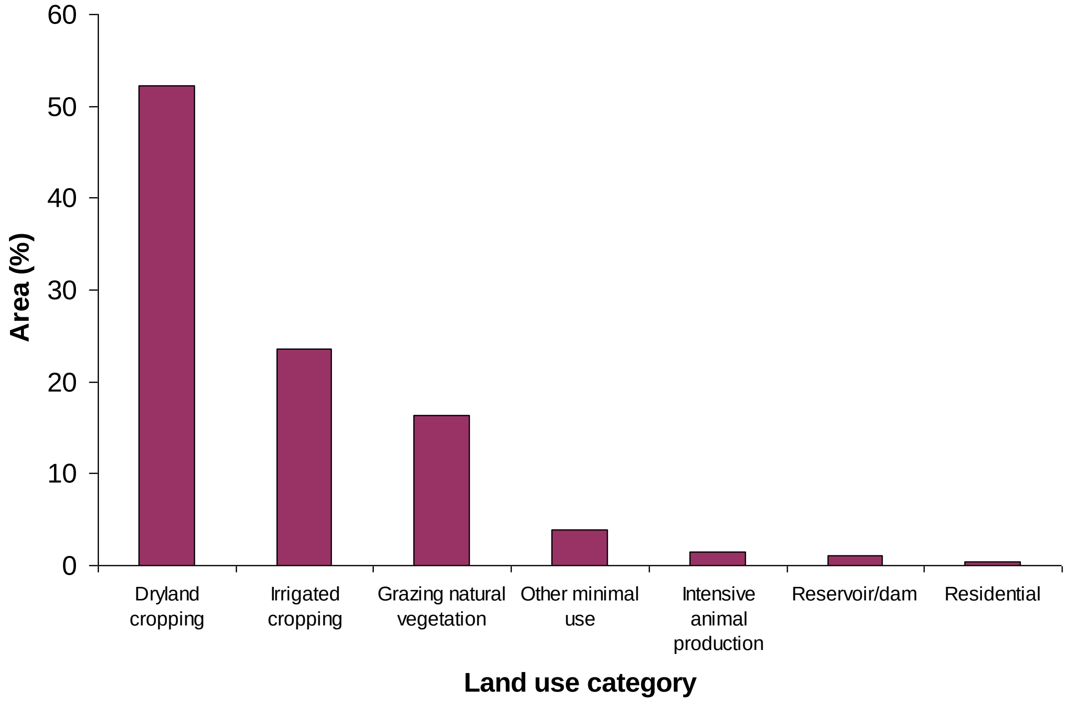


Figure 2.6 Areal extents of different land uses on the Upper Condamine floodplain (Data source: DERM and BRS 1999).

2.2.2 Water resource development on the Upper Condamine floodplain

Since the 1960s, agricultural development, in particular the development of irrigated cropping, on the Upper Condamine has been accompanied and supported by significant water resource development (Thoms and Parsons 2003) to mitigate risk associated with the highly variable rainfall and streamflow of the region (McKay *et al*. 1999, Porter 2002). Water harvested for irrigation currently comprises regulated and unregulated in-stream flows, overland flow (rainfall runoff) and groundwater (Porter 2002). Water resource infrastructure in the Upper Condamine catchment includes Leslie Dam (a 106 GL capacity dam near Warwick and upstream of the Upper Condamine floodplain), a number of small in-stream regulatory weirs (publicly and privately owned), privately owned off-stream water storages, and licensed (irrigation and rural town water supply) and unlicensed (stock-and-domestic) groundwater bores (CSIRO 2008).

Regulation and harvesting of in-stream flows

Regulated and unregulated flows on Upper Condamine section of the river and its major tributaries have been extensively developed for irrigation and are regarded as fully allocated (McKay *et al.* 1999). Total diversions are approximately 31% of total available water (297.3 $\mathrm{GL.yr}^{-1}$), based on modeled mean annual runoff and outflow (DSEWPC 2009), with a nominal 97.2 GL of in-stream surface water flow (30.6 GL regulated and 66.6 GL unregulated) licensed for extraction annually for irrigation purposes (CSIRO 2008).

Flow regulation occurs downstream of Leslie Dam, with the regulated section of the main river channel extending to Cecil Plains Weir (Figure 2.7). In this section, the Upper Condamine Water Supply Scheme (Upper Condamine WSS) provides supplementary flows to service licensed Water Access Entitlements, predominantly for irrigation purposes. Entitlement volumes are nominal and actual allocations and extractions are determined by seasonal water availability (CSIRO 2008). For example, in the 2006/07 and 2008/09 drought years, ‘medium priority’ (most irrigation) entitlements were reduced to 0%, but returned to 96% of nominal volumes in 2007/08 (SunWater 2009, SEC 2010). Harvested water is pumped from the river and diverted to privately owned off-stream storages located in riparian areas adjacent to the river. In 2001, there were 73 of these storages, with a total storage capacity of 53.5 GL, along the supplemented (Upper Condamine WSS) section of the river (Taylor and Meecham 2003).

Nominal entitlements in the Upper Condamine WSS include 14.5 GL diverted to the Condamine North Branch via pipeline from the Yarramalong Weir (Figure 2.7), and distributed to irrigators (McKay *et al.* 1999, DERM 2010a, SEC 2010). The North Branch project was designed to alleviate pressure on local groundwater supplies (BAE 1976), which are significantly impacted by extraction for irrigation purposes (Barnett and Muller 2008, CSIRO 2008). Fifty percent (7.3 GL) of diversions to this project are classed as high priority entitlements (DERM 2010a), and surface water and groundwater entitlements are exchangeable under certain conditions (i.e. managed conjunctively) in this area (DERM 2010a).

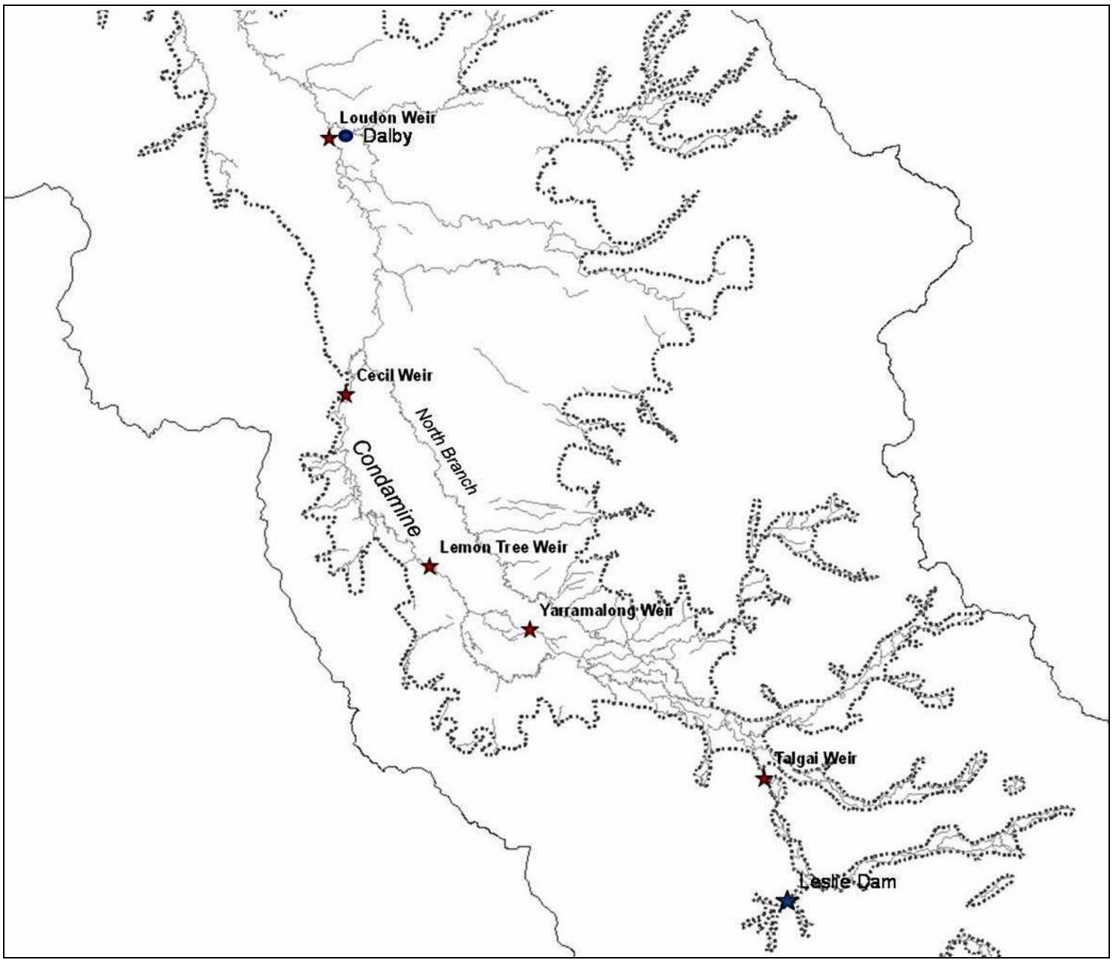


Figure 2.7 Location of key in-stream storage structures on the Upper Condamine floodplain sections of the Condamine River, southern Queensland.

Flow regulation in the Upper Condamine Supply Scheme is managed in response to seasonal conditions and ability to supply to registered users (DERM 2010a). While there is an element of retaining water in the system for environment purposes with ‘no-flow, no-take’ restrictions in unregulated sections (DERM 2010a), a significant shortcoming in water resource planning in the Upper Condamine is a lack of detailed understanding of the water (volumes, dynamics) required to maintain ecological function within riverine and riparian ecosystems (e.g. Arthington and Pusey 2003).

Diversion and harvesting of overland flow

Overland flow includes local on-farm stormwater runoff, general surface runoff from rainfall across the plains where there are no defined watercourses, flow in minor water courses, and overbank flow from major streams during flooding (Taylor and Meecham 2003, CSIRO 2008, DERM 2010a). This is an important component of regional water supply, with significant overland flow volumes currently intercepted and diverted into on-farm storages or ‘ring tanks’ (Porter 2002, Figure 2.8).

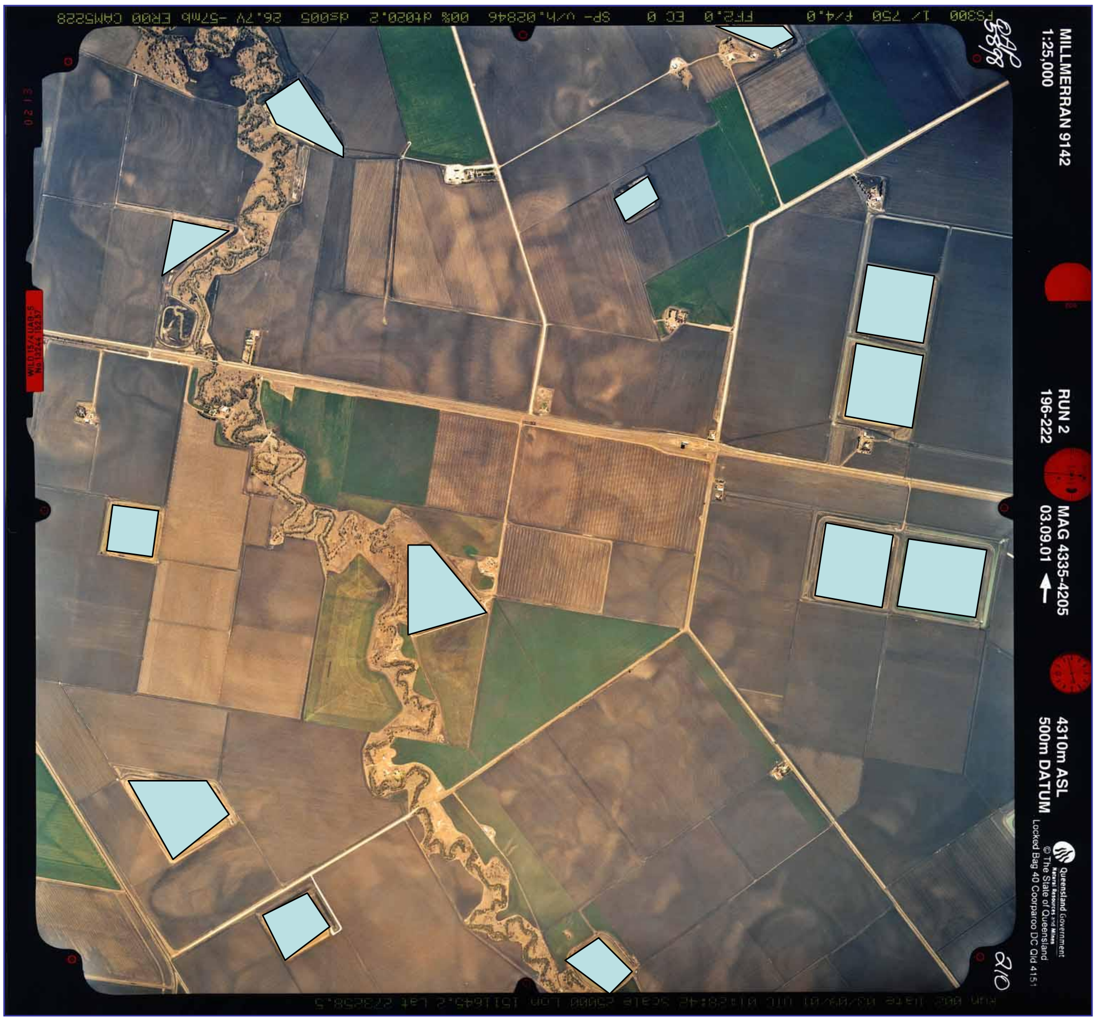


Figure 2.8 Aerial photograph showing floodplain ring-tanks (□), roads, and distribution channels on the North Branch section of the Upper Condamine floodplain, September 2001.

Construction of private off-stream water storages and the capture of overland flow across the Condamine floodplains increased rapidly from the mid-1970s (Porter 2002). Development of private storages, and the diversion, harvesting and storage of overland flow, was poorly regulated until the introduction of a moratorium on the construction of new ring tanks in 2000, and new legislation under the Queensland *Water Act 2000* (Porter 2002). For example, there was a 57% increase in the number, and a 61% increase in total capacity, of private off-stream storages over a period of less than 3 years from early 1997 to late 1999, with a trend towards construction of larger capacity ring tanks (Porter 2002). By 1999, there were some 320 off-stream storages, storing water harvested from in-stream and overland flows (McKay *et al.* 1999, Taylor and Meecham 2003). These had a combined capacity of approximately 170 GL (greater than that of Leslie Dam), and approximately 50% of stored water derived from overland flow (McKay *et al.* 1999). Licensed ring tank capacity in the Upper Condamine is currently 41.9 GL, with volumes harvested limited by the size of the storage and maximum pumping restrictions of 8.4 GL.day^{-1} (CSIRO 2008).

Diversion of overland flow intercepts significant volumes of run-off water, and can significantly reduce flows reaching receiving streams (Porter 2002). Porter (2002) modeled flows in two subcatchments on the Upper Condamine floodplain with and without ring tanks, and reported a 39 to 62% reduction in flows reaching receiving streams. Porter (2002) predicted that a further 50% increase in total storage volume from 1999 levels would result in an additional 9% (approximately 23.5 GL) reduction in average annual flows at Macalister at the downstream end of the Upper Condamine floodplain.

Similarly, roads, rail corridors, irrigation channels, fence lines and crop strips represent significant impediments to historical overland flow paths across the floodplain (Knowles-Jackson and McLatchey 2002, Taylor and Meecham 2003). There has been limited planning or coordination of floodplain development, and the impact of these changes on local hydrological condition is essentially unknown (Knowles-Jackson and McLatchey 2002, Taylor and Meecham 2003).

Groundwater extraction

Extraction from registered groundwater bores constitutes between 18 and 61% of regional water use in the Condamine-Balonne system (highest in years of low surface water availability) with around 97% of this occurring in the Upper Condamine (CSIRO 2008). Rapid development of regional groundwater resources occurred in the 1960s and '70s, resulting in declining groundwater levels in many areas (Kelly and Merrick 2007, DNRMW 2008). Extraction of groundwater resources in the Condamine Alluvium is now regulated within the Condamine Groundwater Management Area, consisting of five sub-areas known as Groundwater Management units or GMUs (Porter 2002, Kelly and Merrick 2007). However, despite regulation, groundwater usage of up to 54 GL.year^{-1} across the Condamine GMUs in the ten years to 2006 exceeded estimated viable (sustainable) yields by between 20 and 60% (Kelly *et al.* 2006). Annual groundwater extraction from the Condamine Alluvium currently exceeds recharge (modeled at between 31 and 36 GL.year^{-1}) in over 90% of modeled years (Barnett and Muller 2008, CSIRO 2008).

Significant development of groundwater resources is evident in the study area. In 2003, there were 3,533 current groundwater authorisations in the Upper Condamine region (Free 2003, cited in Kelly *et al.* 2006). There are also an estimated 25% more unregistered (non-irrigation 'stock and domestic') bores in the region (CSIRO 2008). Extraction pressure on groundwater resources varies spatially across the floodplain (Table 2.1), in response to soil type and level of floodplain development (i.e. relative proportions of dryland and irrigated agriculture), the availability of alternative water sources (e.g. surface water and overland flow harvesting), and water quality. For example, extensive floodplain development on good quality cropping soils, in combination with good quality (low salinity) groundwater, in the area between Brookstead (near Yarramalong Weir) and Dalby (GMU Sub-Area 3, encompassing the North Branch area) has resulted in high levels of groundwater extraction (Table 2.1). The opposite is true of parts of the floodplain with limited development due to constraints such as soil type or water quality (e.g. GMU Sub-Area 5) (Table 2.1).

Table 2.1 Groundwater entitlements and annual extractions in relation to modelled sustainable yields, and average salinity across the 5 Groundwater Management Units (GMUs) of the Upper Condamine Groundwater Management Area. (Source: DSEWPC 2009).

GMU*	**Area**	**Total Water Allocated**		**Total Water Used**		**Sustainable Yield**	**Avge salinity**
	km2	ML/yr	% of sustainable yield	ML/yr	% of sustainable yield	ML/yr	mg/l
Sub-area 1	305	3,560	250%	2,157	150%	1,440	2,302
Sub-area 2	500	10,723	430%	3,436	140%	2,490	656
Sub-area 3	1,280	49,562	335%	18,323	125%	14,810	537
Sub-area 4	500	3,694	190%	1,284	65%	1,930	548
Sub-area 5	1,020	1,126	75%	155	10%	1,500	11,263

*** Sub-area 1:** Dalby to MacAlister (north of the river); **Sub-area 2:** Cecil Plains to Mirrabooka (south of the river); **Sub-area 3:** Brookstead to Dalby (east of the river); **Sub-area 4:** Leyburn-Brookstead; **Sub-area 5:** Millmerran to Cecil Plains (west of the river)

Groundwater levels on the Upper Condamine floodplain have been monitored since the 1960s (DNRMW 2008, DSEWPC 2009). Monitoring bores close to the river generally maintained levels (with minor fluctuations in response to rainfall and streamflow) until the 1990s (Figure 2.9a). However, many bores, particularly those at greater distance from the river, have shown a steady decline in groundwater depth levels since recording began, in some cases in the 1960s (Figure 2.9b–d). Significant decline of between 6 and 20 m is evident from 1990 onward in the majority of bores in Sub-Area 3 (Table 2.1), extending east of the river from Brookstead (near Yarramalong Weir) to Dalby (DSEWPC 2009). Declining groundwater levels have been of particular concern in this GMU and, particularly, in the North Branch area, where extraction levels well in excess of estimated sustainable yields have resulted in a significant depression under the floodplain and disconnection of the alluvial aquifer from surface flows in the main river channel (Barnett and Muller 2008, CSIRO 2008). This section of the river (i.e. downstream from Yarramalong Weir; Figure 2.7) is classed as under ‘maximum losing’ condition. However, little of this lost surface flow contributes to groundwater recharge due to the loss of connectivity and resulting thickness of unsaturated sediments beneath the river (Barnett and Muller 2008). This is in contrast to the section upstream of Yarramalong Weir (the Talgai-Yarramalong reach; Figure 2.7) in which high losses from surface flows are a major source of groundwater recharge to the alluvial aquifer (CSIRO 2008). New coal seam gasfield developments across the northern Murray Darling Basin, including the Condamine catchment, are likely to exacerbate pressure on groundwater resources (Moran and Vink 2010).

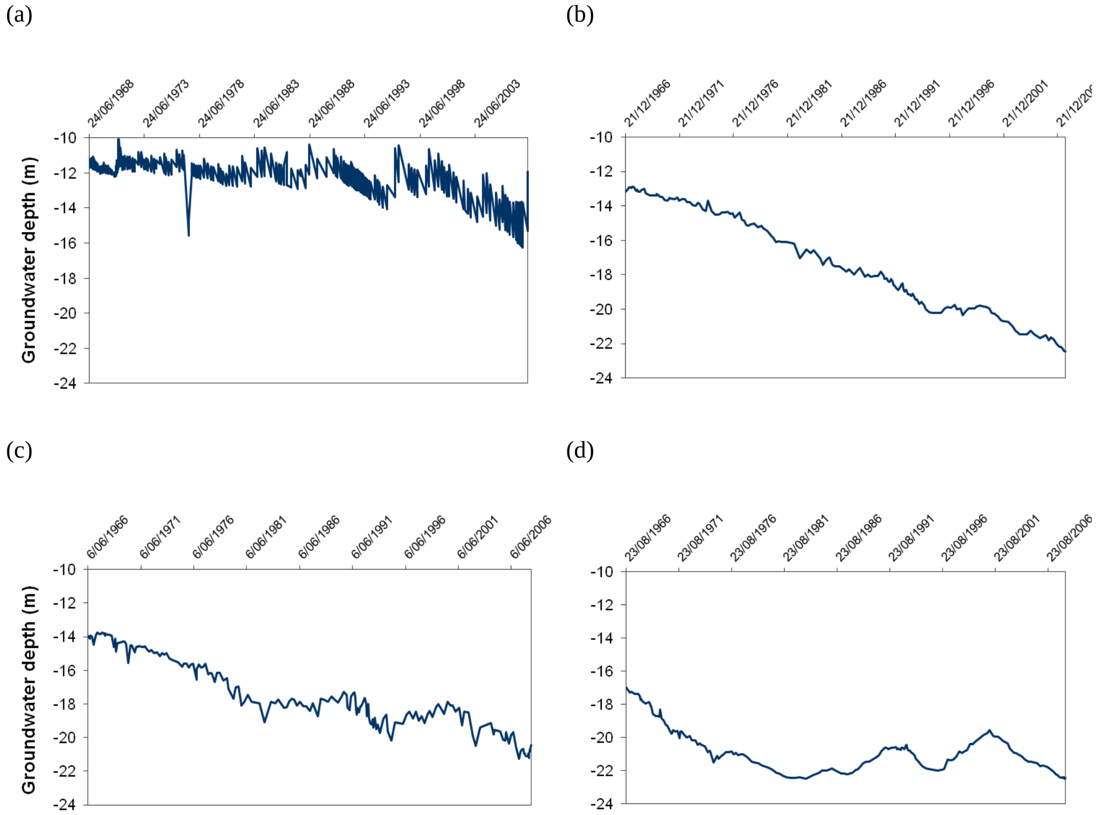


Figure 2.9 Groundwater trends in selected bores: (a) #42230060; (b) #42230071; (c) #42230061; (d) #42230069, within the Queensland Department of Environment and Resource Management groundwater monitoring network (DNRMW 2008). Bores were chosen to show the range of responses within the alluvial aquifer associated with the main Condamine River channel.

Altered hydrological regimes

Changes in the spatial and temporal aspects of the Condamine-Balonne's hydrology associated with development have been investigated under modelled 'reference' (no regulation, abstraction or catchment development) and 'current' (1999–2000 water resource and catchment development conditions) scenarios (Sheldon *et al.* 2000, Thoms and Parsons 2003). Modelling by Sheldon *et al.* (2000) indicated that water resource development in the Condamine-Balonne has resulted in a 140% increase in the frequency of no flow periods, a 69% reduction in the frequency of low flows, and a 59% reduction in the frequency of medium and high flows compared with natural (predevelopment) flows. Thoms and Parsons (2003) concluded that the hydrological character (e.g. magnitude and frequency of flood events and low flows) of the mid-zone (which includes the Upper Condamine floodplain section) of the river is significantly altered under the current water-resource development scenario, with evidence of reduced spatial and temporal heterogeneity. These studies are in agreement with findings from studies in other river systems (e.g. Gaeuman *et al.* 2005, Nilsson *et al.* 2005, Thoms *et al.* 2005) which indicate that water-resource development alters the hydrological character of rivers at the whole-of-river system scale (Ward 1998). However, Thoms and Parsons (2003) comment on the difficulty of determining the impacts of development on the hydrological regime based on historical data in the Condamine-Balonne, given the rapid rate of water resource development and the naturally variable flow regime of the river. This view is reiterated by the recent CSIRO Sustainable Yields report for the Condamine-Balonne (CSIRO 2008).

Modeling of hydrological condition in the Condamine-Balonne under different climate change scenarios indicates that runoff in the region is more likely to decrease than increase; the 'best estimate 2030 climate' indicates reductions of 8% in surface water availability and 5% in average surface water diversions, an increase in the period between floods but a reduction in flood magnitude, and a decline in groundwater recharge (CSIRO 2008). As above, estimates are constrained by lack of consistent and comprehensive long-term hydrological data for the region (CSIRO 2008).

2.2.3 Land cover change on the Upper Condamine floodplain

Floodplain sections of the catchment were originally covered by extensive floodplain grasslands and grassy open woodlands (EPA 2005). Land use change associated with agricultural development on the floodplain has resulted in significant land cover change, with over 75% of native vegetation converted to cropping (dryland and irrigated) land uses (Figure 2.6). Of the remaining native vegetation, most has been subject to some level of selective clearing, pasture modification or grazing pressure associated with livestock enterprises (Phillips and Moller 1995, Fensham 1998a, Sattler and Williams 1999).

Currently, less than 5% of vegetation cover on the Upper Condamine floodplain remains as mapped native remnants (EPA 2005), and a number of vegetation types (Regional Ecosystems or REs) are identified as of significant conservation concern (Sattler and Williams 1999, DERM 2009). Extensive Queensland bluegrass (*Dichanthium sericeum*)-dominant grasslands (RE 11.3.21) originally covered 55.8% (over 272,000 ha) of the Upper Condamine floodplain, but have been largely converted to cropping land (Fensham 1998a, Sattler and Williams 1999, Goodland 2000). The mapped area of remnant grassland on the floodplain is now 2,450 ha, just 0.9% of the pre-European extent (EPA 2005), and this ecosystem type is currently listed as 'critically endangered' under the Australian Government *Environmental Protection and Biodiversity Conservation Act 1999.*

Clearing for agriculture has also contributed to a significant reduction in the extent of grassy woodland ecosystems systems on the floodplain. Poplar box (*Eucalyptus populnea*) woodlands (RE 11.3.2, Sattler and Williams 1999) currently occupy less than 5% (approximately 5,500 ha) of their original (pre-European or pre-clearing) extent (114,290 ha), and are at risk of further decline due to patch degradation and altered population processes (Batterham 2008). Riparian *E. camaldulensis/E. tereticornis*-dominant ecosystems (REs 11.3.25 and 11.3.4, Sattler and Williams 1999) have been reduced to 14.3% (6,275 ha) of their 43,900 ha pre-clearing extent on the Upper Condamine floodplain (EPA 2005). All three of these floodplain woodland ecosystems types are currently classed as 'of concern' (Sattler and Williams 1999, DERM 2009).

Extent of riparian woodlands

Riparian *E. camaldulensis/E. tereticornis*-dominant woodlands (REs 11.3.25 and 11.3.4, Sattler and Williams 1999) once formed a continuous belt of fringing (riparian) vegetation along the floodplain sections of the main river channel and its major tributaries (EPA 2005). Mapped as "Tall woodland or open forest of *E. tereticornis* on Cainozoic alluvial plains" (RE 11.3.4; Sattler and Williams 1999) and "Fringing woodlands of *E. tereticornis* or *E. camaldulensis* on Cainozoic alluvial plains" (RE 11.3.25; Sattler and Williams 1999), both ecosystem types occur on deep cracking clay soils in association with major watercourses on the floodplain. RE 11.3.4 occurs on alluvial plains and terraces adjacent to water courses, while RE 11.3.25 is more closely associated with streambanks. Both have a prominent perennial grassy understorey, but RE 11.3.4 tends to lack a midstorey while RE 11.3.25 often has a sparse, tall shrub layer dominated by species such as *Acacia salicina* and *A. stenophylla* (Sattler and Williams 1999).

The distribution of these riparian woodland ecosystems is naturally constrained to long linear patches associated with the river channel, its main tributaries and alluvial plains and terraces (Sattler and Williams 1999). Altered extent of these woodlands is largely associated with the narrowing and fragmentation of remnants as floodplain agriculture, in particular irrigated cropping, has developed (Phillips and Moller 1995). Both types are almost universally reduced to a narrow band of trees along the larger watercourses, and mapped as small highly fragmented ecosystem remnants (Sattler and Williams 1999). However, despite their limited extent, *Eucalyptus tereticornis/E. camaldulensis* forests and woodlands are significant features of the floodplain landscape of the Upper Condamine where they are frequently the only remaining native woody vegetation, providing critical habitat and connectivity across the agricultural landscape of the floodplain (DERM 2009).

Condition in riparian woodlands

Riparian woodland remnants on the floodplain are also significantly degraded, with widespread evidence of dieback and high mortality in mature eucalypts, limited recruitment of eucalypt seedlings and locally high abundance of invasive weed species (McCosker 1996, Voller 1998). This decline is of concern to land managers in the region (pers.obs.); however, there is limited understanding of the key drivers of change in these ecosystems and restoration attempts have generally had limited success (Greening Australia 2003).

Investigations into tree decline in these woodlands in the mid-1990s considered a range of potential causes (Voller and Eddie 1995), but failed to identify any primary driver (Voller 1998). Observed changes were attributed to a combination of factors, including repeated defoliation by possums (*Trichosurus vulpecula*), insect attack, damage by sulphur-crested cockatoo (*Cacatua galerita*)/little corella (*C. sanguinea*), drought severity, weed competition, grazing, and intensification of land use (Voller 1998). Salinity was not closely associated with the observed decline (Voller 1998), and hydrological factors (e.g. altered flow and flood regimes, groundwater changes) were not considered. This current research represents a first attempt to better understand the role of changed hydrology, in combination with spatial context and land management, on riparian woodland composition and condition in this highly modified landscape.

2.3 Assessment of environmental condition on the Upper Condamine floodplain

The Upper Condamine floodplain landscape has been significantly modified for agricultural production purposes, with extensive development and intensification of both dryland and irrigated cropping. This has involved significant reduction in the extent of native floodplain vegetation communities, the areal extent of which is well below the nominal 30% threshold thought to be the minimum required to retain biodiversity and ecological function within landscapes (Fahrig 2003, Fischer and Lindenmayer 2007, Walker *et al.* 2009). Little of the remnant extent of these ecosystems is held in reserves, and larger remnants are generally used for grazing production purposes, frequently reported as a key driver of changes in community composition and function (e.g. Clarke 2003, Leonard and Kirkpatrick 2004). A number of previous studies report significant decline in remnant condition in native floodplain riparian woodland ecosystems in this landscape; however, there has been limited investigation of this, and there is little understanding of the proximal drivers of ecological change in this landscape.

While high levels of land use and water resource development are evident in this landscape, attempts to characterise hydrological changes by modeling the impacts of development on hydrological regimes in this system are constrained both by poor records of pre-development flows and the extreme natural variability in the system. Despite this uncertainty, diversion of in-stream flows is thought to have contributed significantly to altered hydrological regimes in this system (Sheldon *et al.* 2000, Thoms and Parsons 2003). Impacts include a reduction in low, medium and high flows and a significant increase (over modeled historical flows) in the duration of no-flow periods (Sheldon *et al.* 2000), effectively compounding the effects of significant climatic variability and leading to a greater degree of ephemerality (and potentially effective drought) in riverine flows in this system (e.g. Jenkins *et al.* 2005). Changes in hydrological characteristics in the Condamine-Balonne river system vary both spatially and temporally, indicating potential for cross-scale interactions and complex ecological responses in this system (Thoms and Parsons 2003).

Along the Condamine-Balonne River, reductions in the magnitude of flows and in the extent and duration of overbank flooding increasingly disconnects parts of the floodplain from the main river channel (Thoms 2003, Sheldon and Thoms 2006b), and limits the soil moisture and nutrient supplementation usually associated with flooding (Thoms 2003). This is further compounded by the construction of roads, levees, storages and other infrastructure, which constrain overbank flooding and divert overland flows from historical flowpaths, limiting connectivity and resource supplementation within riparian areas and across the floodplain (Thoms 2003). Reductions in the frequency and duration of overbank flooding and overland flow diversions also limit deeper infiltration to subsoil and groundwater layers, and may further contribute to groundwater decline (Huxley 1982, Barnett and Muller 2008). While overland flows may make a relatively minor contribution to groundwater recharge in the Upper Condamine due to the high clay content and surface-sealing characteristic of Vertisol soil types (Huxley 1982, Kelly and Merrick 2007), significant localized infiltration occurs on high clay content soil types on the Chowilla floodplain, southern Australia, in association with trees and gilgai (‘melonholes’) (Bramley *et al.* 2003, Holland *et al.* 2006). This indicates that riparian areas may contribute significantly to groundwater recharge where overland flows are not diverted and tree function/groundcover vegetation/soil structure is not compromised.

There is also increasing disconnection of surface and groundwater systems in this system under current development and water management regimes. Increasing ephemerality of in-stream flows in this system constrains groundwater recharge to shallow alluvial aquifers associated with the river channel (Barnett and Muller 2008, Reid *et al.* 2009), while falling water tables contribute, in turn, to reduced baseflow back to surface waterbodies (Barnett and Muller 2008, Reid *et al.* 2009). This situation is compounded by unsustainable groundwater extraction evident in the sections of the river below Yarramalong Weir (Barnett and Muller 2008), the Middle and Lower sections in this study (Table 2.1). While these river sections are classed as under 'maximum losing' condition by the CSIRO (2008) Sustainable Yields report, streamflow losses no longer contribute to groundwater recharge due to increasing disconnection between surface and groundwater systems resulting from unsustainable levels of groundwater extraction (Barnett and Muller 2008, CSIRO 2008). This may have significant implications for water-dependent riparian and floodplain species in this part of the Upper Condamine, particularly during extended drought periods when access to shallow groundwater systems is likely to provide an important buffer against moisture stress (Kerle *et al.* 1992, Tyree *et al.* 1994, Pockman and Sperry 2000).

In contrast to the situation in the southern Murray-Darling system (Holland *et al.* 2006, Overton *et al.* 2006), groundwater quality in the Condamine Alluvium is considered to be good, with relatively low levels of salinity recorded in the majority of monitoring bores (DSEWPC 2009) and limited evidence of soil salinisation on the floodplain sections of the main river channel (Jolly *et al.* 2001, Biggs and Power 2003). Widespread groundwater decline evident in the majority of monitoring bores intercepting these aquifers indicates a relatively low risk of salinisation associated with shallow (and rising) watertables (Biggs *et al.* 2009), although application of poorer quality groundwater for irrigation purposes is still a potential source of induced salinity (Rengasamy and Olsson 1993, Biggs and Power 2003). Poorer water quality (higher salinity levels) in groundwater systems on the left bank of the river (Sub-area 5 in Table 2.1) in part explains the limited development of irrigated cropping on this section of the floodplain.

National and state government moves to deliver environmental water allocations to support water-dependent species and ecosystems are yet to be implemented in the Condamine-Balonne (DERM 2010a). While the need for environmental water allocations in this highly modified system is not questioned, this research does question whether an understanding of system dynamics developed from research conducted predominantly in southern Australia is directly applicable to systems outside that region. Similarly, State government legislation limiting further clearing of mapped remnants and significant local effort invested in revegetation and weed control have had little apparent impact on the condition of these woodlands.

2.4 Current land use and resource condition in the study area

It is apparent from the review above that the Upper Condamine floodplain is a highly developed agricultural landscape exhibiting significant changes in hydrology, land use intensity and native vegetation cover. Native ecosystem remnants embedded in this landscape are significantly reduced in extent and generally reported to be in poor condition. Studies reported in subsequent chapters in this thesis investigate riparian woodland condition along the regulated floodplain section of the Upper Condamine (i.e. the river section, between Talgai and Cecil Plains weirs, receiving supplemental flows through the Upper Condamine Water Supply Scheme). This section of this chapter identifies spatial patterns in land use and resource condition on that portion of the floodplain (i.e. the study area). Specifically, it reports differences in hydrological patterns, as well as water and land use intensity, between the River Section and River Bank treatments which stratify the study area in studies reported in Chapters 3 and 4.

The longitudinal zonation of rivers (both natural and anthropogenic) is well recognised (Chapter 1). Large-scale hydrogeomorphic gradients are evident from constrained upland zones to mobile and meandering zones on floodplains (Thoms and Parsons 2003). At finer scales, river reaches may differentiate into distinct ‘functional process zones’ within riverine ecosystems (Thorp *et al.* 2006). In-stream structures associated with flow regulation are also frequently associated with changes in longitudinal connectivity (serial discontinuity) along rivers (Ward and Stanford 1995a, Stanford and Ward 2001), and to altered flood regimes and lateral connectivity with their floodplains, and subsequent responses in riparian ecosystems (Ward and Stanford 1995b, Ward *et al.* 1999, Thoms *et al.* 2005).

The importance of lateral connectivity associated with overbank flooding is also recognised in the literature (Chapter 1), but rarely investigated in the context of riparian or floodplain (non-wetland) vegetation communities. Lateral connectivity across floodplains is restricted (temporally and spatially) where flood frequencies and magnitudes are reduced by flow modification (Ward and Stanford 1995b, Ward *et al.* 1999). It can also be disrupted by the presence of anthropogenic structures on the floodplain (roads, channels, levees) (e.g. Kingsford 2000, Steinfeld and Kingsford 2008), which constrain both overbank flooding extent and overland rainfall runoff to riverine and riparian environments from upslope parts of catchments. Differences in runoff area, land surface condition, and the presence of structures associated with floodplain development can disrupt historical runoff flowpaths (e.g. Souchere *et al.* 1998, Kingsford 2000, Costelloe *et al.* 2005), potentially influencing floodplain and riparian ecosystem function and condition (Kingsford 2000).

2.4.1 Method of assessment

Study area stratification

The relationship between current hydrological condition, floodplain development intensity (the integrated impacts of land use change, land cover change and resource use) and patterns in vegetation composition and condition was investigated within landscape elements broadly defined by longitudinal and lateral sections of the riparian landscape of the Upper Condamine. On this basis, the study area was subdivided into three river sections (based on the location of stream gauges at Talgai, Yarramalong, Lemon Tree and Cecil Plains weirs) (Figure 2.10, Table 2.2,), and two river bank sections (the Left and Right banks, facing downstream, between Talgai and Cecil Plains weirs) (Figure 2.10).

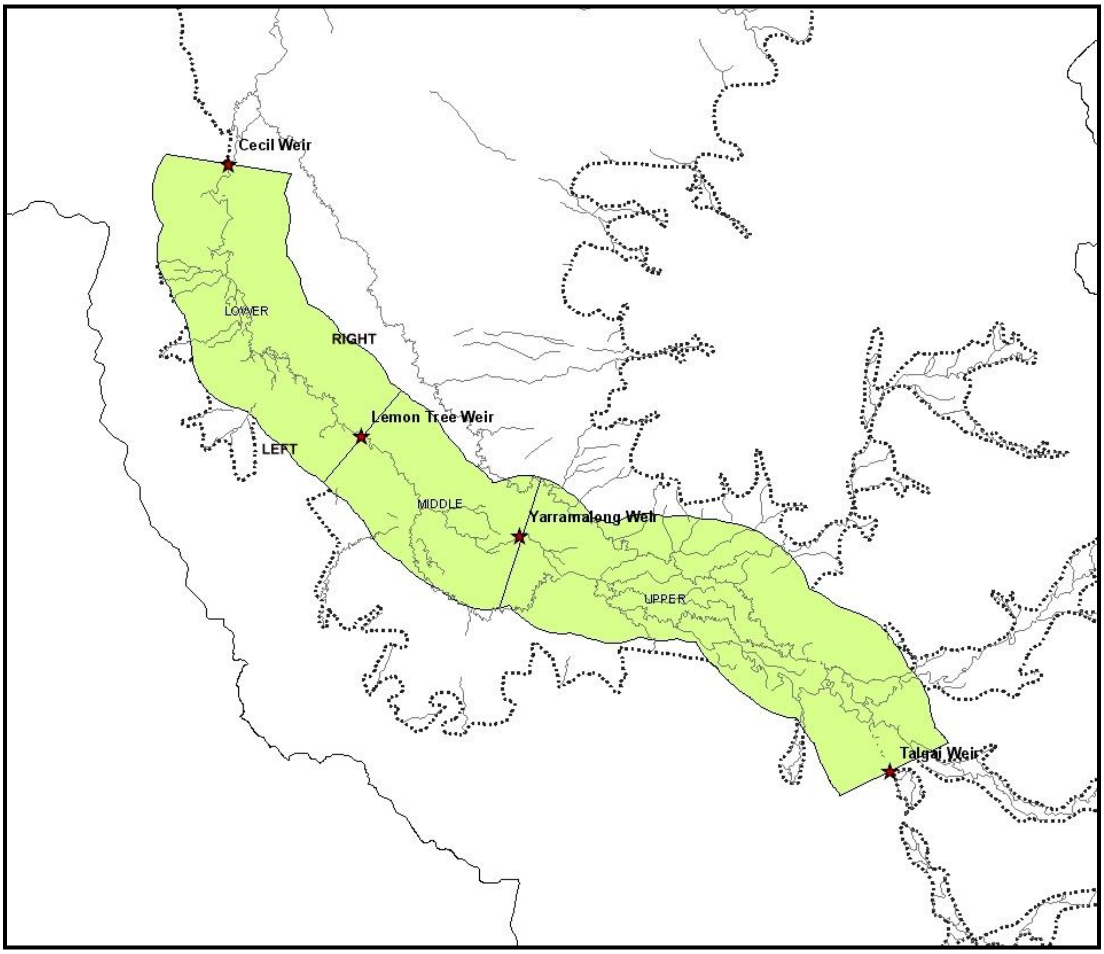


Figure 2.10 River section (Upper, Middle, Lower) and river bank (Left, Right) segments (buffered) on the Upper Condamine floodplain.

Table 2.2 Details of weirs within the Upper Condamine Water Supply Scheme. (Source: DERM 2010a, SEC 2010)

Weir	Constructed	AMTD* (km)	Storage capacity (GL)	Max. regulated discharge (ML.day^{-1})
Talgai	1981	68.6	0.64	740
Yarramalong	1989	131.2	0.39	560
Lemon Tree	1979	154.5	0.30	830
Cecil Plains	1947	206.8	0.70	0

* Adopted Middle Thread Distance (i.e. within channel distance) downstream from Leslie Dam

Data collation

Data presented in the following section were derived from a range of databases held by government departments and resource management bodies. These were in the form either of time-series records, which were analysed in Windows Excel (Microsoft Corporation 2003), or spatially arrayed datasets (data extracted using ArcGIS v9.2; ESRI 2007).

The areal extent of floodplain land uses (cropping, irrigated cropping, grazing, water storages), major flood event extents (1975, 1981, 1988) and native vegetation remnants within river section and river bank segments was quantified within a 5 km buffer extending laterally from the main river channel (Figure 2.10). Values were standardised (i.e. converted to a proportion of buffer segment area) to enable meaningful comparison.

Streamflow data were calculated from the daily time-series datasets (BOM 2010, DERM 2010b, SunWater pers.com.) for the key streamflow gauges at Talgai, Yarramalong, Lemon Tree, and Cecil Plains weirs. Seasonal (summer, winter) streamflow patterns (discharge volumes) are presented by ‘water year’ (i.e. October to September), for the 10 year period preceding this study (i.e. 1995/96 to 2004/05).

Numbers of groundwater bores were derived from the Queensland Government ‘Water Entitlements Register Database’ (DNRMW 2008). Density of bores within the 5 km buffer zone was determined within river section and river bank segments, as above. Floodplain width and catchment width were measured in ArcGIS (above) at 5 km intervals along and perpendicular to the main river channel for each river bank.

2.4.2 Results

Streamflow

Patterns in hydrological parameters were evident across river section (Upper, Middle, Lower) and river banks (Left, Right) segments of the study area. Catchment dimensions for river sections (Upper, Middle, Lower) increase with distance downstream (Table 2.3). Average streamflow volumes correspond to some extent to the geometric increase in cumulative catchment area in the longer-term (1995/96–

2004/05). However, high variability in streamflow is evident between and within these stream sections, with most variability apparent in the Lower (59% of mean annual flow) and least in the Middle (28%) section (Table 2.3). Extended drought conditions were experienced over the 10-year period reported (1995/96 to 2004/05). Extremely low rainfall during the 2004/05 water year (e.g. 476 mm at Dalby; BoM 2010) is reflected in low annual streamflow volumes across all river sections, with no flow recorded for the Middle section at Lemon Tree Weir, and only minor flows recorded for the Upper and Lower sections (Table 2.3).

Mapping of major flooding in 1975, 1981 and 1988 indicates that flood inundation patterns in the study area are highly event-specific, and not consistent within river sections (Table 2.3). The most recent major flood event prior to sampling was in May 1996, when high rainfall resulted in high flows in all stream sections with significant flooding reported across the study area (Taylor and Meecham 2003). However, no flood mapping is available for this event (DERM, pers.com.), and spatial extent of flood inundation was unable to be determined.

Table 2.3 Hydrological details of study area River Sections (Upper, Middle, Lower). Streamflow volumes are end of river section volumes recorded at gauging stations (Upper: Yarramalong Weir; Middle: Lemon Tree Weir; Lower: Cecil Plains Weir). Flood extent (%) is the proportion of 5 km River Section buffers mapped as inundated by major floods (1975–1988). (Sources: Sunwater 2009, DERM 2010b).

River section	**Upper**	**Middle**	**Lower**
Length (km)	62.2	23.6	52.3
Catchment area (km^2)	6,357	7,080	7,795
Cumulative catchment (km^2)	24,717	31,797	39,592
End of river section streamflow volumes (GL/water year ± SE)			
2004/05 (1 yr)	2.70	0.00	0.31
2003/04–2004/05 (2 yrs)	24.2 ± 21.5	9.7 ± 9.7	64.7 ± 64.4
1995/06–2004/05 (10 yrs)	132.1 ± 76.5	242.7 ± 68.7	246.2 ± 145.6
Flood extent (%)			
1988	4	7	10
1981	12	0	0
1975	54	82	52

Flood patterns associated with River Bank sections varied considerably between major flood events (1975, 1981, 1988), and showed no consistent relationship with either differences in catchment and floodplain width on opposite sides of the river (Table 2.4), or the greater rainfall runoff on the right hand side of the river which drains the higher rainfall slopes of the Great Dividing Range.

Table 2.4 Hydrological details of study area River Banks (Left, Right). Flood extent (%) is the proportion of 5km River Bank buffers mapped as inundated by major floods from 1975-1988.

	Left bank	Right bank
Flood extent (%)		
1988	8	5
1981	2	9
1975	69	48

Seasonal streamflow records between 1995 and 2005 indicate variable patterns within and between stream sections. Records from weirs in the Upper and Lower sections exhibit similar patterns with maximum discharges generally occurring in summer months (October–March) and minimal flows in winter months (April–September), with the exception of flooding rains received in May 1996 (Figure 2.11). Records for the Middle (Lemon Tree Weir) section are anomalous, due to significant alteration of flow pattern (volumes and seasonality) associated with flow regulation and redistribution of in-stream flows through the Condamine North Branch irrigation area; Figure 2.11c). Volumes at Cecil Plains Weir reflect the greater downstream catchment area (Table 2.3).

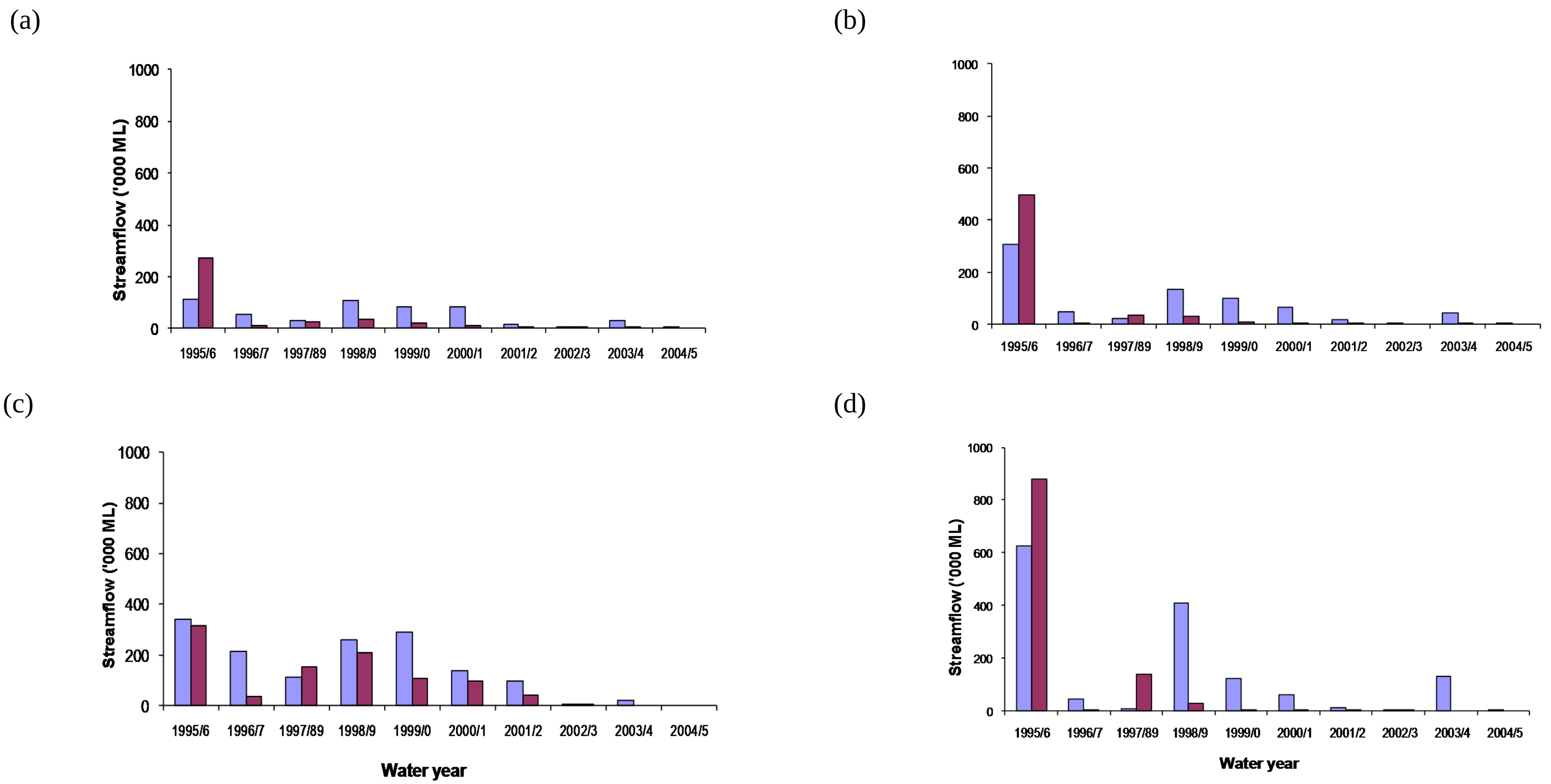


Figure 2.11 Streamflow patterns at (a) Talgai, (b) Yarramalong, (c) Lemon Tree and (d) Cecil Plains weirs by water year (Oct.–Sept.), 1995/96–2004/05. Summer flows (🟪) and winter flows (🟥) are indicated. (Source: DERM 2010b, SunWater 2009).

Data limitations are a significant impediment to more detailed investigation of historical flow and flood patterns in the Upper Condamine. Time-series records are not consistently available across the gauging stations on floodplain sections of the river, commencing in 1947 for Cecil Plains Weir, but in 1990 and 1995, respectively, for Yarramalong and Lemon Tree weirs (DERM 2010b). Other studies have noted the constraints imposed by the limited and inconsistent streamflow record in the Condamine-Balonne catchment to accurately assessing the impacts of water resource and floodplain development (regulation, diversion, extraction) on streamflow (Thoms and Sheldon 2002, Thoms and Parsons 2003) and predicting future impacts of climate change (CSIRO 2008).

Overland flows

Significant capacity to divert and store overland flow associated with rainfall runoff and overbank flooding is evident in the study area. The density of off-stream storages (ring tanks, associated levees and ditches) was greatest in the Middle and Lower river sections (Figure 2.12a), with the greater proportion, and almost six times the area, of these situated on the eastern side of the river (the right river bank) (Figure 2.12b).

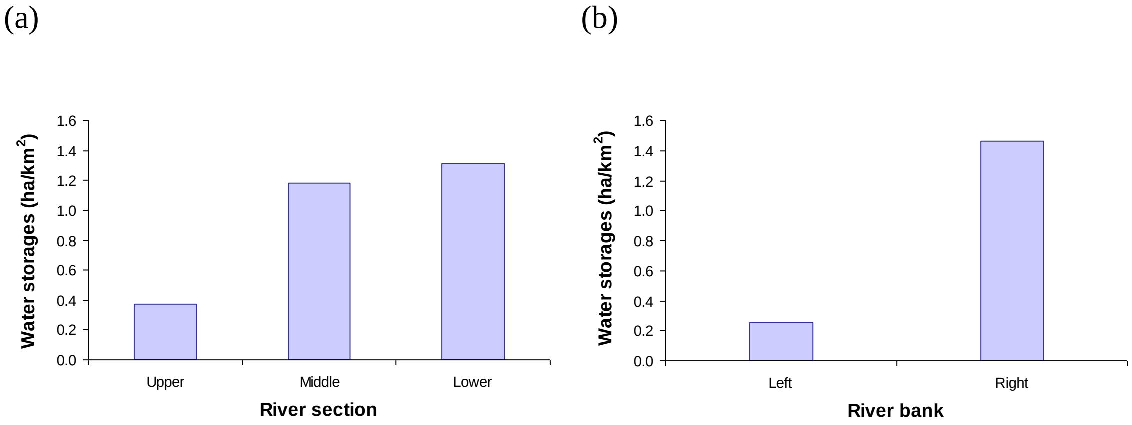


Figure 2.12 Density of irrigation infrastructure (water storages), across (a) river sections (Upper, Middle, Lower) and (b) river banks (Left, Right) within a 5 km zone either side of the river. Data source: DERM and BRS 1999.

Groundwater

A total of 620 registered groundwater bores occur within the buffered sections of the floodplain. The Middle river section (Yarramalong to Lemon Tree weirs) supports the greatest density of these (Figure 2.13a). Similarly, groundwater resources on the right bank of the river are more intensely developed than those on the left (Figure 2.13b), possibly due to the higher average salinity levels associated with groundwater in Sub-area 5 (Table 2.2).

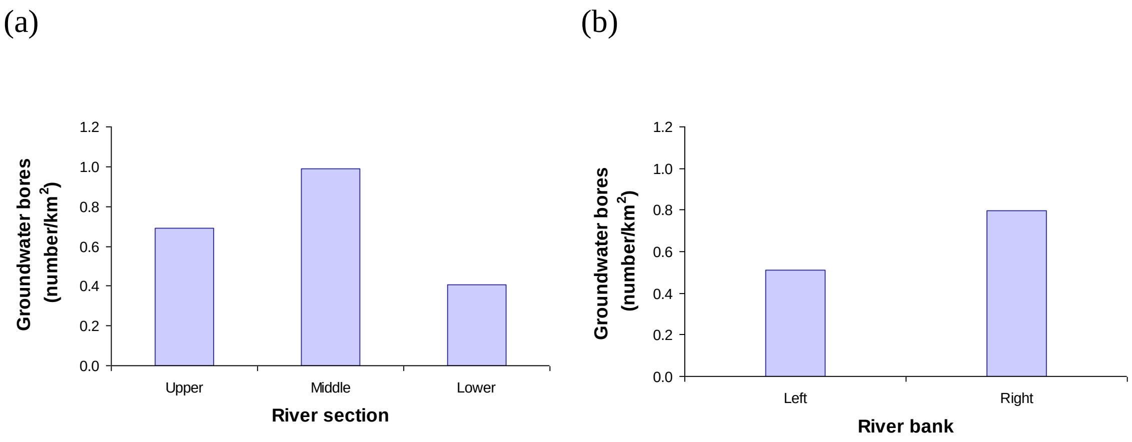


Figure 2.13 Density of registered bores across (a) river sections (Upper, Middle, Lower), and (b) river banks (Left, Right) within a 5 km zone either side of the river. (Data source: DNRMW 2008)

Land use and land cover patterns

Differences in the proportion of land cover and land use types are evident at the River Section scale. The Middle river section (Yarramalong-Lemon Tree weirs) is most developed, with a greater proportion (86%) of the total area under cropping (dryland and irrigated) (Figure 2.14a), and least grazing and mapped remnant vegetation cover compared to either the Upper or Lower sections (Figure 2.14c). The right side of the river is also more intensely developed with the greater proportion of cropping (in particular, irrigated cropping) land uses, and a lower proportion of natural vegetation (Figure 2.14b, d).

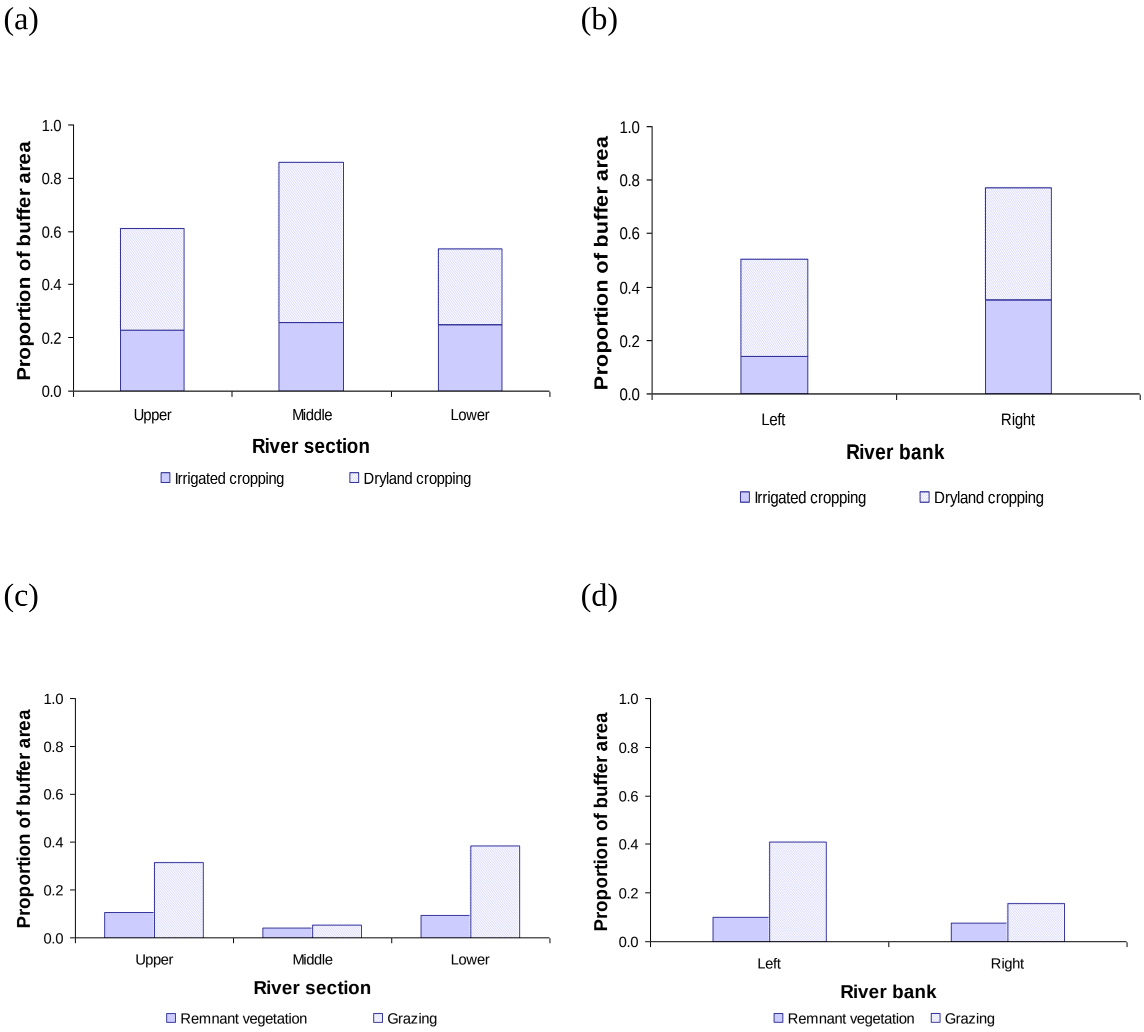


Figure 2.14 Relative proportions of cropping (dryland, irrigated, total), and native vegetation (mapped remnant vegetation, grazed native vegetation), across River Sections (a and c, respectively), and River banks (b and d, respectively) within a 5 km zone either side of the river. Data sources: DERM and BRS (1999).

2.4.3 Discussion

Differences in the hydrology, land cover and intensity of land and water use are evident between River Sections defined by the location of in-stream weirs on the regulated floodplain portion of the Upper Condamine. These include differences in flow volumes and variability, differences in the extent of major flood events, and differences in seasonal discharge volumes in storages between the Upper (Talgai Weir to Yarramalong Weir), Middle (Yarramalong Weir to Lemon Tree Weir) and Lower (Lemon Tree Weir to Cecil Plains Weir) sections.

Differences in land use and land cover variables were also evident across the three River Sections, indicating the potential for confounding influence on ecosystem response. The Middle river section, where flow volumes and variability are least, is also most heavily impacted by floodplain development with the highest levels of cropping and overall water resource development; this section also has the lowest levels of remnant vegetation and grazing land use. The Upper and Lower river sections both support lower levels of cropping and higher levels of grazing and native vegetation cover than the Middle section; however, while floodplain development in terms of the proportion of water storages is greatest on the Lower river section, the density of groundwater bores is least, in contrast to the Upper river section which has limited water storage infrastructure but a relatively high density of groundwater bores compared to the Lower river section.

Differences were also apparent between the Left and Right river banks. Comparisons of hydrological, land cover and land use parameters showed that the Right bank of the river associated with this part of the floodplain is more intensely developed in terms of both land and water use, and supports a relatively smaller proportion of native vegetation. This portion of the floodplain represents the main depositional environment and constitutes the greater area of the floodplain, comprising sediments eroded from the eastern and northern slopes of the catchment (DNR and DoE 1998) under the influence of relatively higher rainfall and rainfall runoff.

2.4.4 Conclusions

The highly developed agricultural landscape of the Upper Condamine floodplain exhibits significant changes in hydrology and native vegetation cover. Native ecosystem remnants embedded in this landscape are significantly reduced in extent and generally reported to be in poor condition. Despite this, riparian remnants are often the only relatively contiguous native habitat remaining on the floodplain, and their persistence is critical to both the retention of biodiversity and provision of a range of ecosystem services in this landscape.

The hydrological regime of the Upper Condamine is governed to a large extent by significant climatic variability, resulting in ephemeral streamflow conditions punctuated by periodic and often widespread flooding, and it is likely that local species are, at least to some extent, adapted to significant environmental variability (Colloff and Baldwin 2010). However, high levels of water resource development have led to substantial changes in surface flows and groundwater levels, often compounding the effects of climatic variability. This has resulted in a more highly disconnected (temporally and spatially fragmented) hydrological system.

Measurable differences in hydrology, land cover and land use occur between river sections and river banks in the study area, and these differences have potential implications for the composition and condition of remnant woodland ecosystems in this landscape. The following chapters investigate whether patterns in riparian woodland composition (Ch.3) and condition (Ch.4) are associated with these broad environmental patterns. Chapter 5 takes a finer-scale approach, focusing on potential drivers of change in these ecosystems by investigating the influence of gradients in hydrology, land cover and land use.

Chapter 3 Patterns in riparian woodland community composition, structure and function on the Upper Condamine floodplain

3.1 Introduction

Many of the world's river systems are under significant pressure to support human populations and activities, with modification of hydrological regimes through impoundment, flow regulation (including flood mitigation) and high levels of water extraction (Arthington and Pusey 2003). Native riparian and floodplain ecosystems along these rivers have evolved in response to disturbance driven by hydrological extremes (flooding, drought) and associated levels of resource availability (Junk *et al.* 1989, Poff *et al.* 1997). However, human activities which appropriate resources (e.g. grazing, irrigated cropping), alter natural disturbance regimes or instigate novel disturbances (e.g. species invasions) contribute to new species combinations and biotic responses in these systems. These changes may introduce new thresholds and result in new emerging (Milton 2003) or 'novel' (Hobbs *et al.* 2006, 2009) states within these ecosystems, with altered system dynamics and resilience to subsequent change. Understanding the relationships between disturbance, ecosystem pattern and underlying ecological processes in these novel ecosystems is critical to sustainable land management, and in particular, biodiversity conservation and ecosystem service provision in landscapes subject to significant anthropogenic change.

3.1.1 Vegetation responses to changes in hydrological connectivity

Hydrological drivers (e.g. overland flows, flood regimes) are considered to be of overriding importance to ecosystem composition and function in riparian and floodplain systems (Thoms and Sheldon 2002, Thoms *et al.* 2005). Studies of riparian ecosystem responses to altered hydrological regimes primarily focus on changes in longitudinal and lateral connectivity associated with in-stream regulatory structures, and, in particular, large dams (e.g. Uowolo *et al.* 2005, Lambs *et al.* 2006). These studies frequently call for water resource management to restore environmental flows which mimic historical hydrological dynamics (e.g. Hughes *et al.* 2001, Stromberg *et al.* 2007a). Such calls are based on an understanding of the direct effects of disturbance, connectivity and resource supplementation on species survival and fitness (e.g. Elger *et al.* 2004), and on community dynamics including succession

(Amoros *et al.* 1987, Corenblit *et al.* 2007). In terms of community composition, flooding disturbance acts as an ecological filter, screening out species unable to tolerate inundation or waterlogging (Poff 1997, Hobbs and Norton 2004, Toogood *et al.* 2008), while decline in the historical frequency, duration and extent of flood events may result in the loss of flood-dependent species (Poff 1997, Hobbs and Norton 2004).

Comparisons of community composition on paired regulated and unregulated rivers indicates homogenization of floodplain riparian ecosystems, with reduced species diversity at both local and landscape scales (i.e. *alpha*- and *beta*-diversity) on regulated streams (Nilsson *et al.* 1991, Nilsson and Jansson 1995, Ward *et al.* 1999, Uowolo *et al.* 2005). Studies using functional trait approaches (specifically, hydrological response groups) also report increasing frequency of flood-intolerant species in riparian woody vegetation with flow regulation and altered hydrological regimes (Burton *et al.* 2009), and changes in proportions of hydric, mesic and xeric annuals with altered seasonal moisture conditions, flooding extent and streamflow permanence (Tabacchi *et al.*1996, Stromberg *et al.* 2005a, 2008). Extended periods without flooding in such systems may lead to drying out of floodplain wetlands (Ward and Stanford 1995), loss of flood-dependent species, and increased richness and abundance of flood-intolerant (terrestrial) species (Marston *et al.* 1995, Nicol *et al.* 2007). Such compositional change infers altered ecosystem function (e.g. changes in infiltration and moisture storage capacity; Rietkerk and van de Koppel 1997), as well as functional change in terms of community response diversity (Capon 2003, Bezemer *et al.* 2006), potentially leaving floodplain systems increasingly vulnerable to further degradation (Boer and Puigdefabregas 2005, Stromberg *et al.* 2007b).

Equally important to ecosystem dynamics and resilience, particularly in systems associated with dryland rivers, are low flow periods. Many perennial species in these systems are adapted to survival during drought conditions which similarly act to screen out less well adapted species (Elmore *et al.* 2003, Gitlin *et al.* 2006). Other species exhibit adaptations to wetting and drying cycles, enabling them to survive (often in the persistent soil seedbank) and respond strategically when conditions are likely to be most favourable for establishment, growth or reproduction (Capon 2003). Significant changes in the frequency, duration and seasonality of drying events contribute to changes in the composition, condition and function of floodplain ecosystems, altering the relative abundance of locally adapted species (e.g. Bren 1992), contributing to increasing homogenization of vegetation patches across a landscape (Stromberg *et al.* 2007a), and potentially reducing the functional diversity of riparian and floodplain ecosystems and their subsequent resilience to drought (Stromberg *et al.* 2007a).

Floodplain development can also influence connectivity across floodplains. For example, flood mitigation levees which limit the extent of overbank flooding effectively act to alienate or disconnect the floodplain from overbank flood flows (Galat *et al.* 1998, Gergel *et al.* 2002a, Kang and Stanley 2005). These are reported to have significant ecological impact in terms of altered soil microbial activity (Kang and Stanley 2005), denitrification rates (Gergel *et al.* 2005), and riparian canopy tree composition (Gergel *et al.* 2002a) and condition (Steinfeld and Kingsford 2008). However, the ecological impact on riparian ecosystems of development infrastructure which diverts or interrupts lateral flow across floodplains to riparian ecosystems is rarely considered. Very few, if any, studies have investigated the impact of such structures on historical overland flows and the transport of nutrients, sediment and plant propagules in storm runoff to riparian ecosystems, although diversion of flood flow paths on floodplains is acknowledged as a potential risk to riparian ecosystems (Porter 2002, Knowles-Jackson and McLatchey 2002), and capture of overland flow as a potential risk to in-stream flows (Porter 2002, Kingsford and Roff 2008).

3.1.2 Vegetation responses to grazing in riparian ecosystems

Livestock grazing is also recognised as a key driver of degradation in riparian ecosystems (Lunt *et al.* 2007b), largely due to the tendency of stock to congregate close to water (Andrew 1988, James *et al.* 1999, Jansen and Robertson 2001). For example, grazed riparian woodlands along the Murrumbidgee River, southern Australia, are reported to have lower biomass of groundcover plants, less litter and particulate organic matter and a higher percentage of bare soil, as well as significantly fewer eucalypt seedlings and saplings, than areas without stock (Robertson and Rowling 2000). As in other landscapes, high grazing intensity alters the composition, structure and function of wetland and riparian communities by reducing the structural complexity and spatial heterogeneity of vegetation and facilitating exotic species invasions (Robertson and Rowling 2000, Jansen and Robertson 2001, Hopfensperger *et al*. 2006).

Interactions between grazing and resource availability are potentially important in terms of ecosystem stability (Allen-Diaz and Jackson 2000, Wright and Chambers 2002, Lunt *et al.* 2007a), and may result in significant changes in vegetation species composition (Allen-Diaz and Jackson 2000, Wright and Chambers 2002). Soil compaction and reduced plant cover associated with grazing may alter the flow of resources and energy in riverine systems by reducing the capacity of vegetation to slow overland flow rates, and trap sediment and nutrients (Bilotta *et al.* 2007, Schacht and Reece 2008), potentially contributing to changes in community composition and function (Stromberg *et al.* 2007a, Beauchamp and Stromberg 2008). State shifts in low or reduced productivity riparian systems may lead to increasing resistance and resilience in the degraded state (e.g. due to altered soil condition, hydrology or a depleted seedbank) and limited recovery in vegetation condition (cover, richness and composition) with grazing exclusion (Lunt *et al.* 2007b).

While river regulation and livestock grazing are both regarded as significant drivers of declining riparian condition, they are only rarely considered in conjunction (e.g. Meeson *et al.* 2002). Robertson and Rowling (2000) warn that restoration efforts that focus only on reducing the impact of altered flow regimes may be less than successful if livestock grazing is not considered as part of river ecosystem management, although Westbrooke *et al.* (2005) suggest that disturbance associated with major flood events is likely to override grazing impacts in floodplain riparian systems.

3.1.3 Study overview

This study investigated key community patterns in riparian woodland composition in relation to landscape-scale hydrological (longitudinal and lateral connectivity) and local-scale land use (grazing) factors associated with the highly modified intensive agricultural landscape of the Upper Condamine floodplain. Riparian remnants in this landscape are associated with an ephemeral river system subject to flow regulation and significant levels of water resource extraction (in-stream flows harvesting, overland flow diversion and harvesting, groundwater extraction) to support irrigated agriculture in the highly modified surrounding landscape. The region is also subject to significant climatic variability (Chapter 2), which is likely to increase with ongoing climate change (Hughes 2003).

Riparian woodland remnants on the Upper Condamine floodplain are reported to be in poor condition (Phillips and Moller 1995, Voller 1998), with significant dieback and limited recruitment of the dominant canopy species, *Eucalyptus camaldulensis/E. tereticornis*, and locally significant populations of the functionally important alien plant species, *Phyla canescens* (lippia). While these broad issues are well recognised, more detailed changes in riparian woodland composition and function in this landscape have not been investigated. Nor are mechanisms of ecological change in this landscape well understood. Significantly, management efforts over recent decades (e.g. weed management, grazing management, tree planting to address poor recruitment and survival of riparian eucalypts), as well as State vegetation clearing laws to protect the extent of native ecosystem remnants, have not noticeably redressed ecological decline in this system. A better understanding of vegetation responses to biophysical conditions associated with current levels of development, in conjunction with prevailing climatic conditions, will contribute to management aimed at enhancing ecosystem resilience and ecosystem service provision in this highly modified production landscape.

This study asks whether current perceptions regarding key drivers of response dynamics in remnant floodplain riparian ecosystems subject to modified hydrological regimes are applicable in a highly modified production landscape. It takes a natural experimental approach (Diamond 1983) to test hypotheses relating to river flow, overland flow and land use. Specifically, the study investigates whether there are significant effects of longitudinal and lateral connectivity (i.e. between river section and between river bank treatments, respectively) and within-remnant land use (i.e. the presence or absence of livestock grazing) on the floristic composition and community structure of remnant riparian woodland ecosystems on the Upper Condamine floodplain.

3.2 Methods

3.2.1 Site selection

Remnant floodplain riparian woodlands along a 150 km section of the Condamine River were sampled between January and April in the summer of 2004–2005. A total of 24 sites was selected from mapped (EPA 2003) and unmapped remnants, verified in the field as *Eucalyptus camaldulensis/E. tereticornis*-dominant fringing or floodplain woodlands (Regional Ecosystems 11.3.4 and 11.3.25, Sattler and Williams 1999) associated with the main channel of the Condamine River (Figure 3.1). All sites were on private properties involved in agricultural production (cropping or grazing). Sampled remnants were characteristically linear configurations aligned with the river channel (mean remnant or riparian width was 355.0 ± 51.2 m and ranged from approximately 75 to 975 m), embedded in a contrasting matrix of irrigated and dryland cropland.

The study area and survey sites were stratified *a priori* by (i) river section (Upper, Middle, Lower); (ii) river bank (Left, Right), and (iii) within-remnant land use (Grazed, Ungrazed by domestic livestock). River section strata corresponded to the scale of stream-flow data (end-points are streamflow gauging stations at in-stream weirs indicated in Figure 3.1) and were designed principally to capture longitudinal or ‘reach’ differences in drainage, streamflow, surface-groundwater exchange, and water use patterns for this stretch of the river (Thoms and Parsons 2003, CSIRO 2008). However, these hydrological influences cannot be isolated from the associated land use/land cover context in this landscape. Hence, the study also effectively investigates vegetation patterns associated with differences in development intensity across these three river sections (Chapter 2). Similarly, River bank treatments capture differences in factors influencing lateral overland flow parameters on opposite sides of the main river channel. These are associated with variables influencing runoff such as floodplain extent, land use and land cover, and water-harvesting infrastructure (diversion channels, ringtanks), while floodplain hydrogeomorphology will also influence over-bank flooding patterns (Steiger and Gurnell 2003, Thoms 2006). Within-remnant land use was used as a third treatment factor, to enable investigation of patch-scale management impacts on vegetation composition and condition, as well as potential interactions between hydrology and grazing. Table 3.1 indicates the distribution of sites. (Further details are provided in Appendix A). Replication in some groups was constrained by a lack of suitable remnants in this relictual landscape.

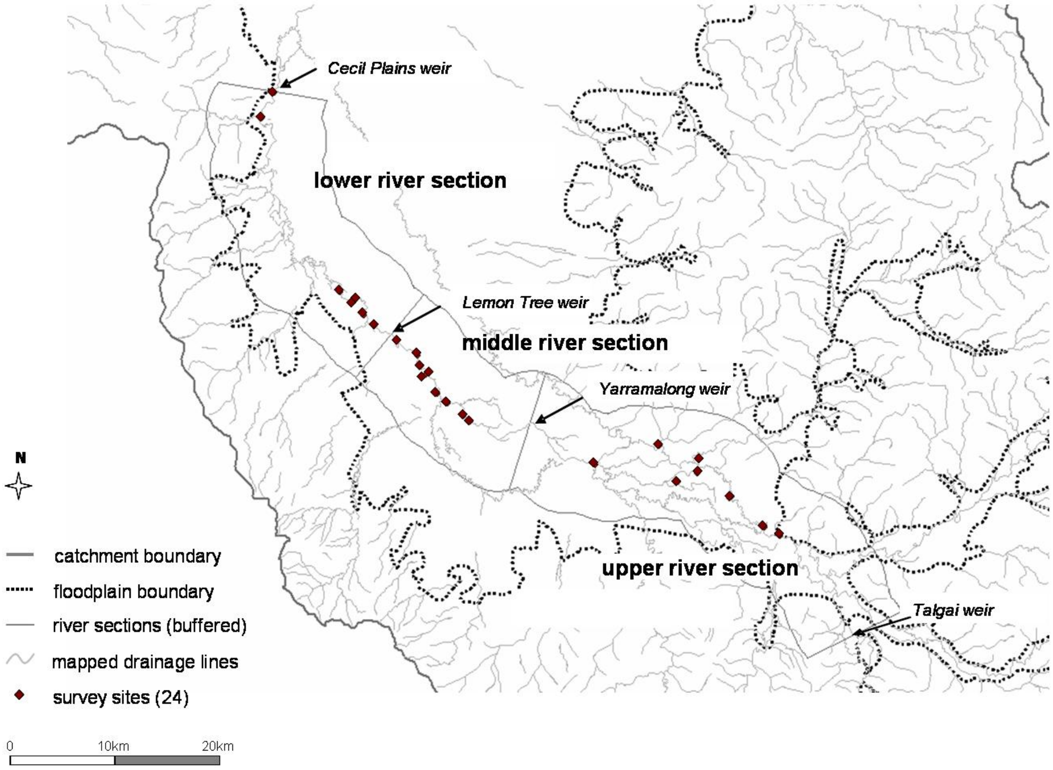


Figure 3.1 Upper Condamine floodplain study area, indicating survey site locations and the location of weirs defining the end-points of river section treatments.

Table 3.1 Distribution (number) of survey sites per sampling stratification category (stream section, riverbank, land use). Weir and site locations are indicated in Figure 3.1.

River section	Reach (defined by in-stream weirs)	River bank		Land use		Total
		Left	Right	Grazed	Ungrazed	
Upper	Talgai – Yarramalong	3	5	6	2	**8**
Middle	Yarramalong – Lemontree	4	5	3	6	**9**
Lower	Lemontree – Cecil Plains	3	4	1	6	**7**
Total		**10**	**14**	**10**	**14**	**24**

Sampling locations

Sample sites within remnants were selected according to predetermined criteria. Those on the same side of the river were at least 500 m apart in different remnant patches or management units (to reduce spatial autocorrelation due to proximity of sites), in a representative patch of vegetation near the centre of the remnant (in terms of distance from the river channel) and, where possible, at least 40 m from both the river channel and the remnant edge to limit edge effects (e.g. Thorburn and Walker 1994).

Auto-correlation (spatial, temporal) of observations is a potential issue in studies where survey sites are not effectively independent at all relevant ecological scales (Wintle and Bardos 2006, Lawrence Lodge *et al.* 2007). While efforts were made to minimise this at the local patch scale, patterns related to precipitation (for example) across the study area could not be effectively managed and were assumed to be random. The study design in this case is inherently auto-correlated as river sections are related (effectively, nested catchment areas) in terms of location, and patterns which conformed to the order of river sections were interpreted cautiously.

Site details

For each site, location and elevation were recorded by hand-held GPS (easting, northing, UTM reference, altitude). Distances from river, remnant edge and property boundary were either measured or estimated (if greater than 100m). Patch condition and context were visually assessed for each site. Details recorded included landform (floodplain, terrace), current within-patch land use, evidence of site disturbance and adjacent land use(s). Evidence of site disturbance (clearing, fire, grazing, weed control, flooding, erosion and mechanical disturbance was scored on a 5 point intensity scale (after Batterham 2008) (Table 3.2).

Table 3.2 Site disturbance categories and scoring (after Batterham 2008)

Disturbance	**Type (evidence)**	**Intensity**
Clearing	Selective (stumps), mechanical (windrowed)	No evidence (0) – severe (4)
Fire	Recent, past (fire scars etc)	No evidence (0) – severe (4)
Grazing	Native, domestic, feral (tracks, dung)	No evidence (0) – severe (4)
Flooding	Recent (waterlogging, debris), past (flood scours)	No evidence (0) – severe (4)
Other	Erosion, mechanical disturbance	No evidence (0) – severe (4)

No significant differences for clearing, fire or soil disturbance scores were identified across river section, river bank or land use treatments (Kruskal-Wallis and Mann-Whitney U, $p > 0.05$; Table 3.3). Grazing scores differed significantly across river sections ($p \leq 0.05$) and land use groups ($p \leq 0.005$), but not river banks ($p > 0.05$). Grazing (native and domestic animals) was significantly greater at Upper section sites than Middle, with Lower section sites intermediate ($p \leq 0.05$), and at Grazed sites than Ungrazed ($p \leq 0.005$). Significantly higher scores for evidence of previous flooding were recorded for left bank than right bank sites ($p \leq 0.05$), but there was no significant difference in flooding between river sections or land use groups ($p > 0.05$, Table 3.3).

Table 3.3 Measures of site condition and woodland structure by site groupings (river section, river bank, land use). Treatment values are means and standard errors (in parentheses). Significant differences within treatment factors are indicated in bold type; values sharing the same superscript are not significantly different ($p > 0.05$).

Treatment factor	**River section**[1]			**River bank**[2]		**Land use**[2]	
Treatment level	**Upper**	**Middle**	**Lower**	**Left**	**Right**	**Grazed**	**Not grazed**
Number of sites	8	9	7	10	14	10	14
Site condition							
Clearing (score: 0 – 4)	0.9 (0.5)	0.3 (0.2)	1.4 (0.3)	0.8 (0.2)	0.9 (0.3)	1.0 (0.4)	0.7 (0.2)
Fire (score: 0 – 4)	0.3 (0.2)	0.4 (0.2)	0.3 (0.2)	0.5 (0.2)	0.2 (0.1)	0.2 (0.1)	0.4 (0.2)
Grazing (score: 0 – 4)	**1.9^{a} (0.4)**	**1.0^{b} (0.2)**	**1.1^{ab} (0.1)**	1.5 (0.3)	1.2 (0.2)	**1.9^{a} (0.3)**	**0.9^{b} (0.1)**
Flooding (score: 0 – 4)	0.3 (0.3)	0. 6 (0.3)	0.0 (0.0)	**0.7^{a} (0.3)**	**0.0^{b} (0.0)**	0.4 (0.3)	0.2 (0.2)
Soil disturbance (score: 0 – 4)	0.5 (0.3)	0.2 (0.2)	0.0 (0.0)	0.4 (0.3)	0.1 (0.1)	0.4 (0.2)	0.1 (0.1)
Woodland structure[3]							
Trees > 20m (FPC%)	**5.8^{a} (1.9)**	**0.3^{b} (0.2)**	**6.4^{ab} (4.1)**	4.2 (1.7)	3.7 (2.2)	4.2 (1.6)	3.7 (2.2)
Trees 10 to 20m (FPC%)	7.6 (1.7)	5.4 (0.8)	5.9 (2.1)	5.7 (1.8)	6.7 (0.9)	6.4 (1.5)	6.2 (1.1)
Trees < 10m (FPC%)	**0.5^{a} (0.3)**	**2.4^{a} (1.2)**	**6.9^{b} (2.0)**	3.1 (1.4)	3.1 (1.2)	**0.7^{a} (0.4)**	**4.8^{b} (1.3)**
Shrubs > 2m (FPC%)	0.1 (0.1)	0.0 (0.0)	0.6 (0.6)	0.0 (0.0)	0.3 (0.3)	0.0 (0.0)	0.3 (0.3)
Shrubs 1 to 2m (FPC%)	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)	0.1 (0.0)
Shrubs < 1m (FPC%)	0.7 (0.4)	6.4 (3.4)	1.9 (0.9)	2.8 (1.6)	3.5 (2.1)	3.6 (2.9)	2.9 (1.1)
Forbs (FPC%)	42.4 (5.5)	31.8 (7.2)	35.1 (8.9)	35.3 (7.0)	37.0 (5.2)	37.6 (8.2)	35.4 (4.2)
Graminoids (FPC%)	49.3 (6.2)	50.6 (5.3)	54.3 (8.3)	61.5 (6.8)	51.0 (4.1)	53.4 (7.5)	49.6 (3.4)
Logs > 30cm (FPC%)	1.4 (0.5)	1.0 (0.3)	1.3 (0.3)	1.1 (0.3)	1.3 (0.3)	1.0 (0.3)	1.4 (0.3)
Logs 10 to 30cm (FPC%)	1.0 (0.3)	0.9 (0.1)	1.1 (0.3)	0.9 (0.2)	1.0 (0.2)	1.1 (0.2)	0.9 (0.2)
Woody litter < 10cm (FPC%)	0.8 (0.2)	0.9 (0.2)	0.7 (0.3)	0.9 (0.2)	0.7 (0.2)	0.6 (0.2)	0.9 (0.2)
Non-woody litter (FPC%)	47.6 (11.9)	66.1 (6.1)	66.0 (11.7)	70.1 (8.5)	52.7 (7.3)	54.1 (10.8)	64.1 (6.2)
Bare ground (FPC%)	1.9 (0.7)	2.1 (1.0)	1.6 (1.4)	1.2 (0.6)	2.4 (0.9)	2.2 (1.0)	1.7 (0.8)

[1] Kruskal-Wallis (MannWhitney U); [2] MannWhitney U; [3] non-parametric analyses due to heteroscedastic variances for many variables (unable to be corrected by data transformation)

Structural composition

Vegetation structure within a 1,000 m^2 sampling quadrat was subjectively determined by estimating projected cover (%) for trees (>20 m, 10-20 m, <10 m), shrubs (>2 m, 1-2 m, <1 m), forbs, graminoids, logs (>30 cm diameter, 10-30 cm diameter), woody litter (<10 cm diameter), non-woody litter, rocks and bare ground (after Le Brocque and Buckney 1997).

There were significant differences in the cover of trees greater than 20 m in height and trees less than 10 m in height across river sections (Kruskal-Wallis, $p \leq 0.05$; Table 3.3), and for trees less than 10 m in height between land use treatments (Mann-Whitney U, $p \leq 0.05$). The cover of trees greater than 20 m high was significantly higher for Upper river section sites than Middle river section sites (Mann-Whitney U, $p \leq 0.05$); Lower river section sites were intermediate and not significantly different from either Upper or Middle river section sites ($p > 0.05$), although there was greater variability in tall tree cover at Lower river section sites (standard error = 4.1). Upper and Middle river section sites had significantly lower cover of trees less than 10 m high than Lower river section sites ($p \leq 0.05$), and grazed sites also had significantly lower cover of smaller trees less than 10 m high than ungrazed sites ($p \leq 0.05$). There were no significant differences in other measures of woodland structure across river section or land use treatments, and no significant differences between river banks (Table 3.3).

3.2.2 Data collection

Floristic composition

Floristic composition was assessed using a modified 1,000 m^2 nested quadrat system (Morrison *et al.* 1995) comprising seven concentric square subquadrats (cumulative areas: 1, 2, 5, 10, 100, 500 and 1,000 m^2). All vascular plant species rooted in a quadrat were recorded and assigned a frequency score (0 to 7) based on the number of subquadrats in which they were found. This method limits sampling bias due to non-random dispersion (e.g. clumping) of organisms, enables higher detection rates of rare species than standard quadrat sampling methods, and provides a reasonable approximation of species density and improved ability to detect patterns particularly in species-poor communities (Morrison *et al.* 1995). It has been successfully adopted in a number of studies to investigate vegetation community patterns (e.g. Le Brocque and Buckney 1997, King and Buckney 2002, Clarke 2003, Lewis *et al.* 2008, Le Brocque *et al.* 2009). Frequency methods are generally appropriate to the investigation of ecosystem response to disturbance as minor species, which constitute the bulk of site diversity and system redundancy (Walker 1992), are more heavily weighted compared to cover abundance methods (Lavorel *et al.* 2008).

A key weed species investigated in this study was the introduced invasive species, *Phyla canescens* (lippia), which has been present in the Upper Condamine since 1927 (Lucy *et al.* 1995, Earl 2003). Lippia is a flood-tolerant perennial clonal C3 forb. It is capable of both sexual and asexual reproduction, and its propagules (seed and vegetative fragments) are readily dispersed by floodwaters. It proliferates rapidly on moist heavy clay soils, such as occur on the Upper Condamine floodplain, particularly where the cover of competitive native species (e.g. tussock grasses) is reduced by disturbance or overgrazing, and has been of significant concern to the grazing industry, particularly in riparian and floodplain pastures in the northern Murray-Darling Basin (Lucy *et al.* 1995, Earl 2003). It is also widespread and highly abundant in this landscape (pers. obs.).

As a result, cover of herbaceous groundcover species (including lippia) was also estimated in four 1 m^2 quadrats randomly positioned within each quadrant of the largest 1,000 m^2 quadrat above. This was necessary as the nested quadrat frequency score method fails to pick up differences in the abundance of very common over- or evenly dispersed species due to saturation effects common to all frequency methods (Morrison *et al.* 1995). Randomisation was by pairs of random numbers pre-generated using an online randomiser.

3.2.3 Data treatment

Floristic composition

Plant species identifications were based on Stanley and Ross (1983, 1986, 1989), Harden (1990–1993) and Sharp and Simon (2002), and verified against specimens in herbarium collections at the University of Southern Queensland, Toowoomba and the Queensland Herbarium, Mt. Coot-tha. Current nomenclature was updated according to the Australian National Botanic Gardens' Australian Plant Name Index (ANBG

2009). Observations for three pairs of closely related species which could not readily be distinguished were combined. These were (i) *Eucalyptus camaldulensis* and *E. tereticornis* (referred to as *Eucalyptus camaldulensis*), (ii) *Einadia nutans* and *E. polygonoides* (referred to as *Einadia* spp.), and (iii) *Eriochloa procera* and *E. pseudoachrotricha* (*Eriochloa* spp.). *Eucalyptus camaldulensis* and *E. tereticornis* can be similar in form and not readily distinguishable unless fruiting (the distinguishing characteristic is the operculum on flower buds) (Doran and Burgess 1993, McDonald *et al.* 2009). They have also been noted to interbreed when occurring in close proximity creating a hybrid type which has intermediate characteristics (Butcher *et al.* 2002, 2009). *Einadia nutans* and *E. polygonoides* were readily distinguished when fresh fruit was present, but less so from leaf form which can be variable and similar (Harden 1990). *Eriochloa procera* and *E. pseudoachrotricha* were difficult to distinguish unless grain was present.

A number of broad functional response groups were identified on the basis of traits associated with responses to disturbance (flooding and grazing), and resource availability. Species were then assigned to a total of ten different (but not mutually exclusive) response groups on the basis of physiology (C3, C4), life history (short-lived, perennial), growth form (forb, tussock grass, clonal), and habitat preference (wetland, floodplain, terrestrial) (Table 3.4) on the basis of information available from the literature and other sources (Appendix B). Native and alien species were treated equally. Within functional groups, alien species may be expected to perform similar or complementary functions to native species (Hobbs *et al.* 2006, 2009). Richardson *et al.* (2007) suggest that it is legitimate to include both native and alien species in an analysis of ecosystem function. This is particularly so for highly modified systems, where alien propagule pressure is typically high and both natural and anthropogenic disturbances promote invasion (Hobbs and Huenneke 1992, Richardson *et al.* 2007).

Table 3.4 Selected functional groupings, including categories within groups, gradient reflected and reported responses.

Group	**Categories**	**Environmental gradient(s)**	**Response**	**References**
life history	short-lived, perennial	nutrient availability	annual and short-lived species favoured under high nutrient conditions	Chapin 1980; Prober *et al.* 2002b, 2005; McIntyre & Lavorel 2007
		disturbance	annual and short-lived species favoured under high levels of disturbance, including grazing	Dorrough *et al.* 2004a,b; McIntyre & Lavorel 2001, 2007
life form	forb, graminoid	disturbance	forbs benefit where limits to grass production exist (e.g. under grazing)	Lavorel *et al.* 1999 a,b; McIntyre & Lavorel 2001; Fay *et al.* 2003
physiology	C3, C4	water availability	C4 species favoured over C3 species under water-limited conditions due to their high intrinsic water use efficiency	Epstein *et al.* 1997; Yu *et al.* 2005
clonality	clonal	grazing	high resprouting capacity favoured with grazing disturbance; long distance clonal growth forms (i.e. plants producing rhizomes or stolons) favoured in disturbed sites	Fahrig *et al.* 1994; Kleijn & Steinger 2002; McIntyre & Lavorel 2007
		resource availability/risk	clonal species well adapted for finding and occupying gaps in heterogeneous environments	De Kroon & Hutchings 1995; Stuefer & Huber 1999; Rosenthal & Lederbogen 2008
habitat	wetland, floodplain, terrestrial	flood disturbance	flood-tolerant and intolerant (terrestrial) species composition and abundance provide consistent indication of flooding regime	Turner *et al.* 2004; Lite *et al.* 2005
		water availability	mesic (wetland) and xeric (terrestrial) species composition and abundance sensitive to water availability	Lite *et al.* 2005

Functional group approaches to investigating ecosystem responses to disturbance provide insight into the mechanisms driving change in multi-species communities, particularly in disturbance-driven and invasion-prone systems such as riparian communities (Richardson *et al.* 2007). Sorting species into functional response groups relevant to the type of disturbance under investigation thus facilitates critical examination of compositional change which may relate directly to emergent ecosystem function (or dysfunction) and indicate potentially critical changes in ecosystem dynamics/resilience. Reduced richness, abundance or associated diversity in functional response groups may indicate a loss of resilience (functional redundancy *sensu* Walker 1992) within communities to environmental change, and suggests that these groups might be most responsive (and potentially vulnerable) to changes in this landscape.

Floristic and functional group indices

Species richness (S: the number of species per sample area) and diversity (H': Shannon-Wiener diversity index) were calculated for total species, total native species and total alien species in the 1000m^2 quadrat. Cumulative abundance (N) indices were calculated by summing over frequency data (nested quadrat scores). Richness, abundance and diversity measures for the functional response groups listed in Table 3.4 were also calculated.

3.2.4 Statistical analyses

Multivariate analyses

Variation in community composition was investigated using the PRIMER software package v5.2.9 (PRIMER-E Ltd. 2002, Clarke and Gorley 2001). The sites by species matrix of frequency data was converted to a matrix of similarities using the Bray-Curtis similarity coefficient. The dataset was standardised but not transformed as it was already effectively geometrically scaled (Morrison *et al.* 1995). Analysis of Similarity (ANOSIM) was used to investigate differences in community composition between river section, river bank and land use treatments. Significant interaction between groups (2-way crossed ANOSIM) was addressed by averaging the test group across the interacting group (Clarke and Gorley 2001). Results of pairwise tests (ANOSIM) were interpreted using Global R values due to the relatively small number of samples (Global R > 0.75 indicated well separated; > 0.5, overlapping but clearly separated; < 0.25, barely separable: Clarke and Green 1988, Clarke and Gorley 2001). Similarity percentage (SIMPER) analyses were used to identify the relative contributions of species to identified patterns (similarity within and dissimilarity between site groupings) (Clarke and Warwick 2001).

Univariate analyses

Community response variables (species richness, abundance and Shannon-Wiener diversity of total, native and alien species, and functional groups), were compared across treatments (river section, river bank, land use) using the 3-way Analysis of Variance (3-way ANOVA) procedures in SPSS version 18.0 for Windows (SPSS Inc. 2009). Prior to analysis, bounded (proportional) data were arcsine transformed, and all data were screened and transformed (either square root or $\log_{10}$), where required, to meet assumptions of normality and homoscedascity (Quinn and Keogh 2002). Where heteroscedastic variances were unable to be corrected for by transformation, no further analysis was undertaken. Where variances were homogeneous (Levene's), 3-way ANOVA was conducted and Tukey's unplanned multiple comparison procedure with Bonferroni adjustment for unequal sample size (Day and Quinn 1989) was used to determine significant difference between treatment pairs in treatments with significant main effects. Where there was significant interaction between river section, river bank and land use treatments, results indicating significant main effect differences were not able to be interpreted (Zar 1999); however, major patterns were explored graphically.

Pearson's correlation procedure in SPSS version 18.0 for Windows (SPSS Inc. 2009) was used to investigate the strength of association between native and alien species richness, abundance and Shannon-Wiener diversity. Prior to analysis, bounded (proportional) data were arcsine transformed, and all data were screened and transformed (either square root or $\log_{10}$), where required, to meet assumptions of normality and homoscedascity (Quinn and Keogh 2002).

3.3 Results

3.3.1 General floristics

A total of 131 vascular plant species was recorded in this survey, of which 95 (72.5%) were native and 36 (27.5%) alien (Appendix C). Of these, the five most frequently recorded species were the alien *Phyla canescens* (present at all 24 sites), and natives, *Einadia* spp., *Eucalyptus camaldulensis*, *Dichanthium sericeum*, *Cyperus gunnii* and *Elymus multiflorus* (each recorded at 23 sites). The five most abundant species were the alien species *Phyla canescens* (with a mean within-site frequency of 6.9 ± 0.1), and the natives *Einadia* spp. (4.9 ± 0.6), *Cyperus gunnii* (4.2 ± 0.5), *Dichanthium sericeum* (3.7 ± 0.5) and *Eriochloa* spp.1 (3.3 ± 0.5).

3.3.2 Patterns in community composition

No significant interaction was evident in overall floristic composition between river section and river bank or river section and land use treatments (2-way crossed ANOSIM, $p > 0.05$); however, there was a significant interaction between river bank and land use treatments ($p \leq 0.05$). There was a significant, but limited, difference in community composition between river sections (ANOSIM: Global $R = 0.196$, $p = 0.002$; Table 3.5) and a significant difference between grazed and ungrazed sites when land use effects were compared within riverbank treatments (2-way crossed ANOSIM, grouping across riverbanks; Global $R = 0.312$, $p = 0.004$), but no significant difference in community composition between left and right river bank groups (Global $R = -0.052$, $p > 0.05$).

Table 3.5 Summary of pairwise tests (ANOSIM) on species abundance data between river section groups. Values are R statistics with significance levels indicated. Significant difference is indicated in bold type (** $p \leq 0.005$, * $p \leq 0.05$).

	Upper	Middle
Middle	**0.207***	-
Lower	**0.223***	**0.168***

Dissimilarity

Differences in the relative abundance of native perennial species contributed most to the dissimilarity between river section treatments (SIMPER, Table 3.6). The alien perennial forb, *Phyla canescens* (lippia), contributed less than 0.5% to dissimilarity between treatment factors (Table 3.6).

Table 3.6 Species contributing to 20% of Dissimilarity between river sections. Lippia (*Phyla canescens*) contribution is also shown. 'Abundance' is frequency recorded across seven nested quadrats (maximum abundance = 7).

Species	**Average abundance**		**Contribution %**	**Cumulative %**
Average Dissimilarity = 62.1	**Upper**	**Middle**		
Einadia spp. 1	4.4	4.7	3.2	3.2
Cyperus gunnii	3.4	5.6	3.0	6.2
Eriochloa spp.	2.4	4.4	2.7	8.9
Dichanthium sericeum	4.6	3.6	2.6	11.5
Panicum decompositum	1.6	2.4	2.6	14.0
Marsilea sp.	4.0	2.8	2.5	16.6
Eulalia aurea	3.3	1.6	2.5	19.0
Paspalidium aversum	2.8	1.4	2.4	21.4
Phyla canescens	7.0	7.0	0.0	-
Average Dissimilarity = 59.0	**Middle**	**Lower**		
Leptochloa divaricatissima	1.8	5.3	4.3	4.3
Cynodon dactylon	1.3	4.9	4.1	8.4
Einadia spp. 1	4.7	5.7	3.5	11.9
Cyperus gunnii	5.6	3.3	3.4	15.3
Paspalidium aversum	1.4	3.0	2.8	18.1
Eriochloa spp.	4.4	3.0	2.7	20.8
Phyla canescens	7.0	6.6	0.4	-
Average Dissimilarity = 62.9	**Upper**	**Lower**		
Leptochloa divaricatissima	1.1	5.3	3.8	3.8
Cynodon dactylon	2.5	4.9	2.8	6.7
Marsilea sp.	4.0	1.9	2.6	9.3
Einadia spp. 1	4.4	5.7	2.6	11.9
Paspalidium aversum	2.8	3.0	2.6	14.5
Cyperus gunnii	3.4	3.3	2.3	16.8
Dichanthium sericeum	4.6	2.9	2.2	19.0
Carex inversa	1.9	2.4	2.2	21.2
Phyla canescens	7.0	6.6	0.3	-

Similarity

Lippia was the most abundant species across all treatments, contributing 18.4%, 20.7% and 15.1% to the Bray-Curtis Similarity (PRIMER SIMPER) within Upper, Middle and Lower river section treatments, respectively; 21.1% and 18.6% in Left and Right river bank treatments, respectively; and 19.5% and 18.0% in Grazed and Ungrazed land use treatments, respectively. The next most influential species were native perennial species (e.g. *Dichanthium sericeum*, *Cyperus gunnii, Einadia* spp.) whose contributions never exceeded 13.3%.

3.3.3 Patterns in community richness, abundance and diversity

Total species richness ranged from 17 to 50 species per 1,000 m^2 quadrat; native and alien species richness ranged from 14 to 35 and 3 to 16 species, respectively (Appendix C).

There was a significant interaction between the river section and land use treatments for total species richness (3-way ANOVA, $p \leq 0.05$; Table 3.7, Figure 3.2a), but no significant interaction between river section and land use treatments for other measures reported in Table 3.7 ($p > 0.05$). There were significant differences in native and alien species richness, and total and native Shannon-Wiener diversity between river section treatments ($p \leq 0.05$). Middle river section sites had significantly lower native and alien species richness and total and native diversity than Upper river section sites ($p \leq 0.05$); Lower river section sites were intermediate ($p > 0.05$). There was no significant difference in species abundance between river section treatments ($p > 0.05$, Table 3.7).

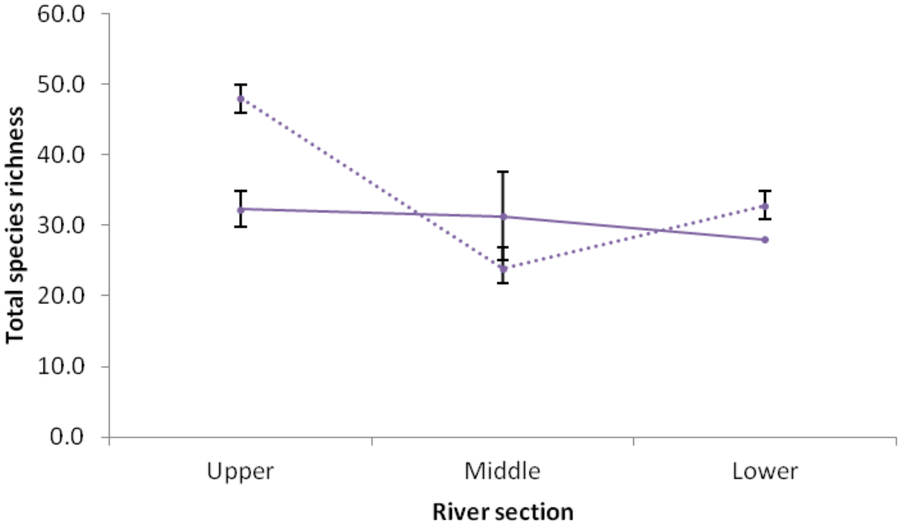
There were significant interactions between river bank and land use treatments for total diversity and native species richness (Figure 3.2b), abundance and diversity ($p \leq 0.05$); interactions patterns were consistent across these measures. No significant interactions were found for total species richness or abundance, or alien species richness, abundance or diversity ($p > 0.05$). There were no significant differences in main effects for richness, abundance or diversity between river bank treatments or land use treatments ($p > 0.05$, Table 3.7).

Table 3.7 3-way ANOVA results for total, native and alien species richness, abundance and Shannon-Wiener diversity by treatments (river section, river bank, land use). Treatment values are means and standard errors (in parentheses). Significant main effects are indicated in bold type; values sharing the same superscript are not significantly different ($p > 0.05$). Interaction values are F statistics with significance indicated in bold type (** $p \leq 0.005$, * $p \leq 0.05$).

	TREATMENTS							**INTERACTIONS**			
	River section (RS)			**River bank (RB)**		**Land use (LU)**		**RS x RB**	**RS x LU**	**RB x LU**	**RS x RB x LU**
	Upper	**Middle**	**Lower**	**Left**	**right**	**Grazed**	**Not grazed**				
n	8	9	7	10	14	10	14				
Total species^1											
S	36.3 (3.2)	26.3 (3.0)	32.1 (1.8)	30.0 (2.7)	32.3 (2.4)	31.6 (2.2)	31.1 (2.7)	0.04	**4.91***	3.78	2.85
N^2	104.5 (10.9)	81.4 (11.0)	95.9 (7.8)	94.4 (10.1)	92.6 (7.8)	93.6 (8.2)	93.1 (8.8)	0.27	2.32	4.33	0.50
H	**3.4^{a} (0.1)**	**3.0^{b} (0.1)**	**3.3^{ab} (0.1)**	3.1 (0.1)	3.2 (0.1)	3.2 (0.1)	3.2 (0.1)	0.13	2.77	**5.37***	3.92
Native species^1											
S	**27.5^{a} (3.0)**	**20.6^{b} (2.2)**	**24.9^{ab} (1.3)**	23.4 (2.2)	24.6 (2.0)	24.9 (2.3)	23.6 (1.9)	0.09	3.27	**5.52***	0.60
N^2	82.6 (11.7)	63.2 (8.7)	73.4 (4.2)	74.0 (8.6)	71.7 (6.9)	75.4 (8.9)	70.7 (6.7)	0.19	2.57	**5.26***	0.15
H^4	**3.1^{a} (0.1)**	**2.8^{b} (0.1)**	**3.0^{ab} (0.0)**	2.9 (0.1)	2.9 (0.1)	3.0 (0.1)	2.9 (0.1)	0.01	3.11	**6.32***	0.35
Alien species^1											
S^3	**8.8^{a} (1.4)**	**5.8^{b} (0.8)**	**7.3^{ab} (1.4)**	6.6 (1.1)	7.6 (1.0)	6.7 (0.9)	7.6 (1.1)	0.24	1.23	0.00	3.85
N^{2,3}	21.9 (2.9)	18.2 (2.8)	22.4 (5.1)	20.4 (3.0)	20.9 (2.7)	18.2 (2.2)	22.4 (3.0)	0.07	0.05	0.08	1.71
H	1.8 (0.2)	1.4 (0.2)	1.7 (0.2)	1.5 (0.2)	1.7 (0.1)	1.6 (0.2)	1.7 (0.1)	0.38	0.54	0.20	3.57

[1] S is species richness, N is total abundance, H is Shannon-Wiener diversity ($\log_e$); [2] arcsin transformed; [3] square root transformed; [4] $\log_{10}$ transformed.

a.



b.

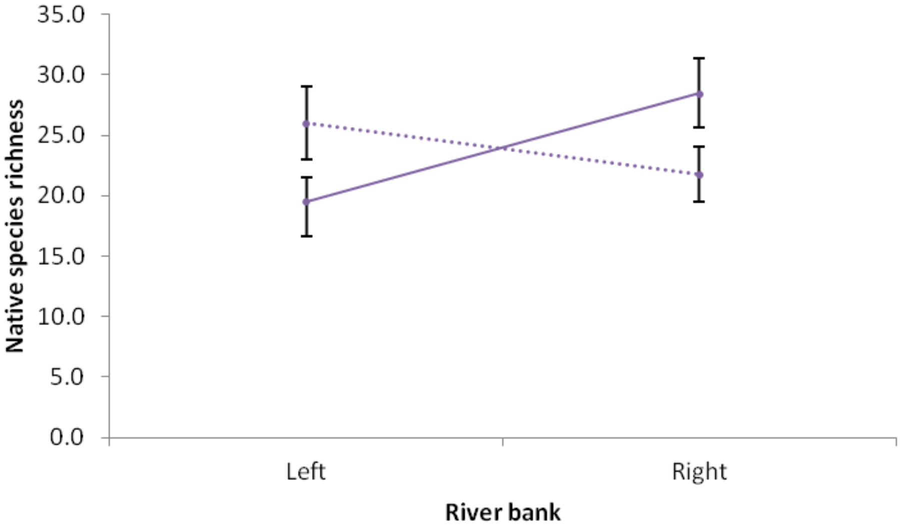


Figure 3.2 Significant interactions between river sections and land use (grazed, ungrazed) for patterns in total species richness (a), and river bank and land use (grazed, ungrazed) for patterns in native species richness (b) on the Upper Condamine floodplain. Values are means for grazed (solid line) and ungrazed (broken line) sites; error bars are standard error.

3.3.4 Patterns in functional group diversity

There were significant interactions between river section and land use treatments for C3, perennial, forb, terrestrial and floodplain species richness and forb Shannon-Wiener diversity, and complex 3-way interactions for tussock grass species and terrestrial species diversity (3-way ANOVA, $p \leq 0.05$; Table 3.8); these conformed with the pattern for total species richness indicated in Figure 3.2a. Heterogeneous variances (Levene's, $p \leq 0.05$) for tussock grass species richness and perennial species Shannon-Wiener diversity could not be corrected by transformation, and further analysis was not conducted on these variables (Table 3.8).

Middle river section sites had significantly lower abundance of forbs and perennial species, and lower diversity of C3 and C4 species than the Upper section ($p \leq 0.05$); Lower river section sites were intermediate and not significantly different from Upper and Middle river section sites for any of these measures ($p > 0.05$, Table 3.8). There was no significant interaction between river section and riverbank or land use treatments for these response variables (3-way ANOVA, $p > 0.05$; Table 3.8).

There were significant interactions between river bank and land use treatments for perennial, forb and wetland species richness, perennial and wetland species abundance and forb Shannon-Wiener diversity, and in all measures for terrestrial species (3-way ANOVA, $p \leq 0.05$; Table 3.8). Interactions patterns were consistent with those of native species richness (Figure 3.2b), with the exception of wetland species richness (Figure 3.3a) and abundance (Figure 3.3b). There were no significant differences in main effects for river bank or land use treatments ($p > 0.05$, Table 3.8).

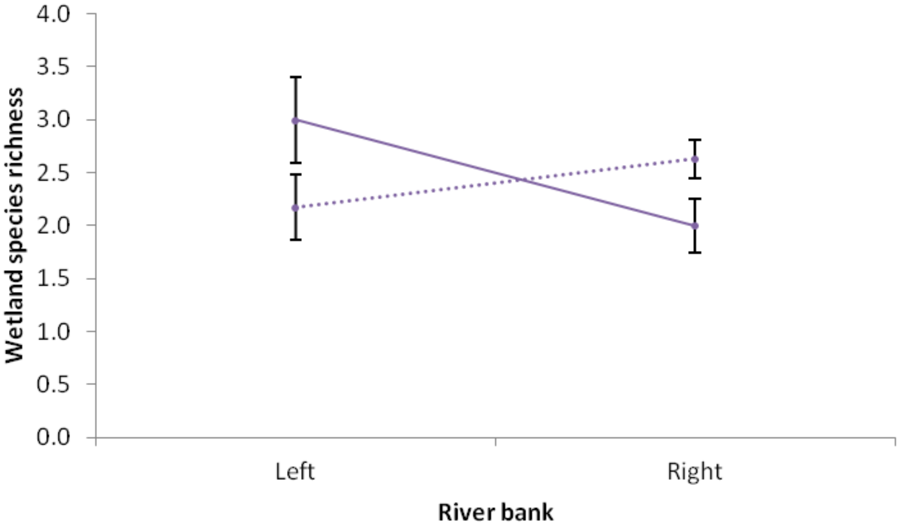
Table 3.8 3-way ANOVA results for functional response group species richness, abundance and Shannon-Wiener diversity by treatments (river section, river bank, land use). Treatment values are means and standard errors (in parentheses). Significant main effects are indicated in bold type; values sharing the same superscript are not significantly different ($p > 0.05$). Interaction values are F statistics with significance indicated in bold type (** $p \leq 0.005$, * $p \leq 0.05$).

	TREATMENTS							**INTERACTIONS**			
	River section (RS)			**River bank (RB)**		**Land use (LU)**		**RS x RB**	**RS x LU**	**RB x LU**	**RS x RB x LU**
	Upper	**Middle**	**Lower**	**Left**	**Right**	**Grazed**	**Not grazed**				
C3 species[1]											
S	19.9 (2.4)	13.0 (1.3)	17.9 (1.4)	15.5 (1.9)	17.6 (1.5)	16.0 (1.3)	17.2 (1.8)	0.41	**6.64***	0.92	1.17
N[2]	52.6 (6.3)	39.1 (4.5)	50.4 (5.5)	45.6 (5.5)	47.9 (4.1)	42.3 (4.3)	50.2 (4.6)	0.11	0.93	1.34	0.15
H	**2.7^{a} (0.1)**	**2.3^{b} (0.1)**	**2.6^{ab} (0.1)**	2.4 (0.1)	2.6 (0.1)	2.5 (0.1)	2.6 (0.1)	0.36	2.37	1.64	1.91
C4 species[1]											
S[3]	11.1 (1.2)	8.6 (1.2)	10.6 (0.6)	9.5 (1.0)	10.4 (0.9)	10.5 (1.1)	9.6 (0.9)	0.06	1.54	2.84	1.30
N[2]	36.6 (4.9)	29.7 (5.9)	37.1 (3.2)	33.9 (4.2)	34.4 (4.1)	37.6 (5.2)	31.7 (3.3)	0.01	2.29	4.62	2.15
H	**2.2^{a} (0.1)**	**1.9^{b} (0.2)**	**2.2^{ab} (0.1)**	2.0 (0.1)	2.1 (0.1)	2.2 (0.1)	2.0 (0.1)	0.08	1.58	3.63	1.54
Perennial species[1]											
S	28.8 (2.5)	18.7 (2.3)	25.1 (1.2)	23.1 (2.5)	24.5 (1.9)	24.9 (2.0)	23.2 (2.2)	0.47	**4.59***	**6.96***	0.98
N[2]	**88.5^{a} (10.1)**	**62.3^{b} (9.0)**	**77.1^{ab} (4.3)**	77.0 (9.1)	74.2 (6.6)	79.8 (7.8)	72.2 (7.2)	0.61	2.77	**5.59***	0.19
H[5]	3.1 (0.1)	2.6 (0.1)	3.0 (0.0)	2.9 (0.1)	2.9 (0.1)	3.0 (0.1)	2.9 (0.1)	-	-	-	-
Short-lived (annual/biannual) species[1]											
S[4]	7.5 (1.2)	7.7 (1.0)	7.0 (1.5)	6.9 (0.8)	7.8 (1.0)	6.7 (0.6)	7.9 (1.1)	0.19	1.21	0.03	2.29
N[2,3]	16.3 (2.8)	19.1 (3.6)	18.7 (5.4)	17.4 (3.4)	18.5 (2.9)	14.0 (1.8)	20.9 (3.4)	0.05	0.22	0.41	1.69
H	1.8 (0.1)	1.8 (0.1)	1.7 (0.2)	1.7 (0.1)	1.8 (0.1)	1.7 (0.1)	1.8 (0.1)	0.28	0.99	0.01	2.40
Forbs[1]											
S	12.9 (1.9)	7.7 (1.3)	10.3 (1.4)	8.9 (1.4)	11.1 (1.3)	10.4 (1.4)	10.0 (1.4)	0.23	**6.91***	**8.03***	0.33
N[2]	**33.3^{a} (4.8)**	**21.0^{b} (2.7)**	**28.1^{ab} (5.2)**	24.1 (4.1)	29.4 (3.3)	25.8 (3.3)	28.1 (3.8)	0.38	2.72	4.66	0.02

	TREATMENTS							INTERACTIONS			
	River section (RS)			**River bank (RB)**		**Land use (LU)**		**RS x RB**	**RS x LU**	**RB x LU**	**RS x RB x LU**
	Upper	**Middle**	**Lower**	**Left**	**Right**	**Grazed**	**Not grazed**				
H	2.2 (0.2)	1.7 (0.2)	2.0 (0.1)	1.8 (0.2)	2.1 (0.1)	2.0 (0.2)	1.9 (0.1)	0.19	**4.49***	**10.68***	1.40
Tussock grasses[1]											
S[5]	11.8 (1.3)	9.4 (1.2)	10.1 (0.3)	10.2 (0.9)	10.6 (0.9)	10.5 (0.9)	10.4 (0.9)	-	-	-	-
N[2]	38.4 (4.8)	33.2 (6.1)	37.1 (3.3)	37.7 (4.9)	34.9 (3.6)	37.5 (4.7)	35.1 (3.7)	0.03	1.13	3.78	1.83
H[3]	2.3 (0.1)	2.0 (0.1)	2.2 (0.0)	2.1 (0.1)	2.1 (0.1)	2.2 (0.1)	2.1 (0.1)	0.14	0.99	2.45	**4.81***
Clonal species[1]											
S	9.0 (0.5)	7.1 (0.7)	7.6 (0.7)	7.8 (0.4)	7.9 (0.6)	8.7 (0.5)	7.3 (0.6)	0.10	3.60	1.07	2.56
N[2]	32.4 (2.0)	24.8 (2.1)	26.6 (3.2)	29.3 (2.3)	26.8 (2.0)	31.8 (1.6)	25.0 (2.0)	0.07	1.49	0.01	0.23
H	2.0 (0.1)	1.7 (0.1)	1.8 (0.1)	1.8 (0.1)	1.8 (0.1)	2.0 (0.0)	1.7 (0.1)	0.12	2.44	0.93	1.29
Terrestrial (generalist) species[1]											
S	24.6[a] (2.3)	15.8 (2.5)	20.7 (2.1)	19.0 (2.1)	21.0 (2.1)	20.9 (1.9)	19.6 (2.2)	0.11	**4.05***	**4.81***	3.23
N[2]	61.6 (7.8)	41.8 (8.7)	53.7 (6.9)	52.0 (7.3)	51.8 (6.5)	53.8 (6.8)	50.5 (6.8)	0.37	2.35	**7.04***	0.49
H	3.0 (0.1)	2.5 (0.2)	2.8 (0.1)	2.7 (0.1)	2.8 (0.1)	2.8 (0.1)	2.7 (0.1)	0.29	1.91	**6.33***	**5.02***
Wetland species[1]											
S	2.3 (0.3)	2.7 (0.2)	2.3 (0.3)	2.5 (0.3)	2.4 (0.2)	2.4 (0.3)	2.4 (0.2)	0.84	0.31	**7.76***	0.61
N[2,3]	8.9 (1.9)	9.8 (1.6)	6.7 (1.7)	10.3 (2.0)	7.4 (0.9)	9.5 (2.0)	7.9 (1.0)	0.03	1.28	**5.07***	0.43
H	0.7 (0.1)	0.8 (0.1)	0.7 (0.1)	0.7 (0.1)	0.7 (0.1)	0.7 (0.1)	0.7 (0.1)	0.59	0.45	3.80	0.34
Floodplain species[1]											
S[4]	11.6 (1.1)	10.6 (0.7)	11.4 (0.6)	11.0 (0.8)	11.3 (0.6)	10.7 (0.6)	11.5 (0.7)	1.33	**3.85***	0.10	1.83
N[2]	43.1 (4.5)	39. 7 (3.3)	42.1 (3.9)	42.4 (3.5)	40.9 (2.9)	40.0 (3.1)	42.6 (3.1)	0.05	0.58	0.04	0.31
H	2.2 (0.1)	2.1 (0.1)	2.2 (0.1)	2.2 (0.1)	2.2 (0.1)	2.2 (0.1)	2.2 (0.1)	0.01	1.26	0.17	0.65

[1] S is species richness, N is total abundance, H is Shannon-Wiener's diversity index ($\log_e$); [2] arcsin transformed; [3] square root transformed; [4] $\log_{10}$ transformed; [7] transformation unable to correct for heteroscedascity (unequal variance).

a.



b.

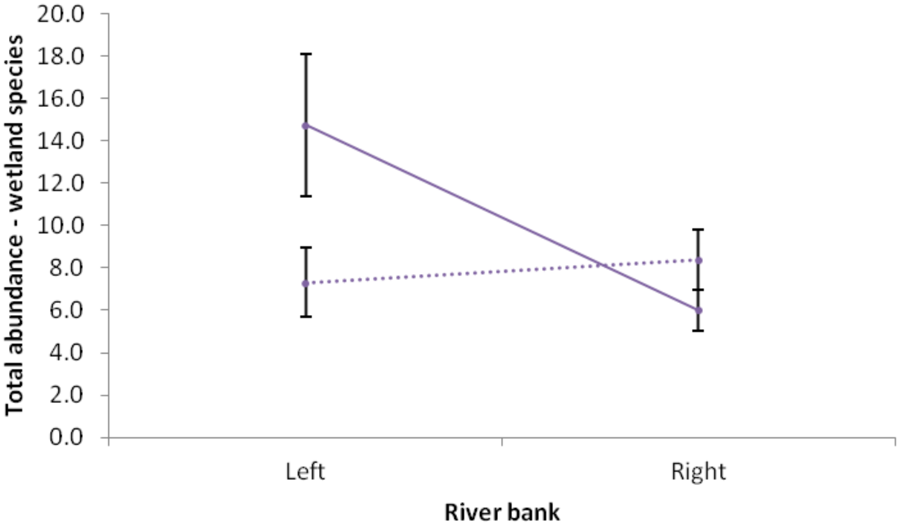


Figure 3.3 Significant interactions between river bank and land use (grazed, ungrazed) for patterns in wetland species richness (a) and abundance (b) on the Upper Condamine floodplain. Values are means for grazed (solid line) and ungrazed (broken line) sites; error bars are standard error.

3.3.5 Patterns in lippia abundance

Heterogeneous variances (Levene's, $p \leq 0.05$) for lippia frequency and cover could not be corrected by transformation, and further analysis was not conducted on these variables (Table 3.9).

Table 3.9 Lippia frequency (1000 m^2 quadrats) and cover (FPC%, 1 m^2 quadrats) by treatments (river section, river bank, land use). Values are means and standard errors (in parentheses).

	TREATMENTS						
	River section			**River bank**		**Land use**	
	Upper	**Middle**	**Lower**	**Left**	**Right**	**Grazed**	**Not grazed**
n	8	9	7	10	14	10	14
Lippia frequency[1,2]	7.0 (0.0)	7.0 (0.0)	6.6 (0.4)	7.0 (0.0)	6.8 (0.2)	7.0 (0.0)	6.8 (0.2)
Lippia cover[1,2]	21.7 (4.6)	12.1 (3.0)	10.1 (2.6)	16.3 (4.1)	13.6 (2.5)	17.3 (4.7)	12.9 (1.8)

[1] arcsin transformed; [2] transformation unable to correct for heteroscedascity

3.4 Discussion

Overall, this study found significant variation in floristic composition and community structure between longitudinal river sections, and significant interactions between river bank and within-patch land use (grazed, ungrazed) treatments in riparian woodland remnants on the Upper Condamine floodplain.

Within river section treatments, and for measures in which significant patterns were detected, Middle river section sites supported consistently lower floristic richness, abundance and diversity than Upper river section sites, while Lower river section sites were consistently intermediate to the other river sections. This pattern was evident for native and alien species richness and total and native species diversity, and for the functional group measures, forb and perennial species abundance and C3 and C4 Shannon-Wiener diversity. These patterns correspond with broad differences in land and water use intensity patterns across the river sections reported in Chapter 2, with the Middle river section exhibiting more extreme hydrological patterns and a greater level of land use development than the Upper river section, while the Lower river section was in many cases intermediate.

No significant patterns in community structure were evident in relation to river bank treatments, despite major differences in floodplain and catchment width and in land use development on opposing sides of the river (Chapter 2). Nor were there significant patterns evident in response to grazing (i.e. within-remnant land use). However, significant interaction between river section, riverbank and within-remnant land use treatments was evident for a number of measures, indicating that community patterns in this landscape may be the result of complex responses to a number of drivers operating at different scales.

Treatments effects on lippia frequency and cover were unable to be analysed in this study due to heterogeneous variances. However, lippia had higher frequency and cover across all treatments than any other species in this study, and contributed more than any other species to floristic similarity and relatively little to dissimilarity between treatment levels, indicating that it was a dominant and widespread species in riparian woodland remnants on the Upper Condamine floodplain, and that its presence had an overall homogenizing effect on floristic composition in these communities.

3.4.1 Pattern in community diversity

Total species richness (131 species) in this landscape was considerably lower than that reported from floodplain landscapes elsewhere (e.g. Pollock *et al.* 1998, Bagstad *et al.* 2005, Aguiar *et al.* 2006, Beauchamp and Stromberg 2008), although the proportion of alien species (28%) was at the higher end of the reported range. For example, Aguiar *et al.* (2006) reported 9% alien richness in floodplain communities in southern Portugal, while Stohlgren *et al.* (1998) found levels ranging from 6 to 24% in riparian communities of the central grasslands in the USA. While low total species richness in this study may, in part, be due to the prevailing drought conditions experienced in the period prior to sampling (BoM 2010, Chapter 2), it may also be indicative of significant degradation in the state of these woodlands as a result of changes in the landscape associated with current levels of development, associated hydrological changes or the prevalence of the dominant invasive alien species, *Phyla* *canescens* (lippia). The legacy of past land use, which involved significantly greater levels of grazing across the landscape and more intense use of riparian ecosystems (e.g. QMDC 2005, Chapter 2), may also continue to influence current community composition as has been reported elsewhere (e.g. Turner *et al.* 2004, Dale *et al.* 2005, Elmore *et al.* 2006b).

The richness of alien species recorded in this landscape indicates, from a community assembly viewpoint, that native ecosystem remnants in this landscape are not particularly resistant to invasion by non-native species (Gilbert and Lechowicz 2005). Non-equilibrial disturbance-driven systems such as riparian communities are inherently prone to invasion (Hobbs and Huenneke 1992), and disturbance, in conjunction with propagule pressure (Foxcroft *et al.* 2007), is widely recognised as a key driver of species invasion (Vosse *et al.* 2008). Disturbances such as flooding, drought and grazing result in stochastic establishment opportunities and fluctuating resource levels which facilitate establishment of species (both alien and locally adapted native species) capable of rapid response to these conditions (Davis and Pelsor 2001, Kreyling *et al.* 2008). Similar response in alien and native species diversity also indicates that both native and alien species in this landscape respond more strongly to environmental gradients than to each other (Shea and Chesson 2002, Deutschewitz *et al.* 2003, Gilbert and Lechowicz 2005). This is in agreement with the Coexistence Theory which proposes that temporal and spatial environmental heterogeneity (e.g. variations in resource availability) increase invasion success (e.g. of opportunistic native and alien species) and promote species coexistence (Davies *et al.* 2005, Melbourne *et al.* 2007, Stohlgren *et al.* 2008). Conversely, environmental filters (e.g. resource limitation, lack of stochastic disturbance), associated with a degraded system and which result in native species loss and subsequent low native niche-saturation levels due to recruitment limitation (Sax and Brown 2000, Moore *et al.* 2001), may also limit invasion success of alien species (Kreyling *et al.* 2008).

Reduced richness, abundance and diversity of native and, to a lesser extent, alien species potentially indicate a more degraded or, at least, a less heterogeneous state (Chapter 1) in the Middle river section of this study. Negligible in-stream flows in this river section in the one and two year periods preceding sampling (Chapter 2), indicate a relatively low level of resources associated with moisture availability, potentially exacerbating prevailing drought conditions. Highly variable flow patterns in streamflow volumes recorded at Lemon Tree Weir over the 10 years prior to sampling indicate considerable variability and altered seasonality in the Middle river section compared to the Upper and Lower sections. However, in this instance, it is likely that these influence only a small portion of this river section (that immediately upstream of the weir), and do not represent flow within the full reach due to the confounding influence of the Condamine North Branch Project (Chapter 2); the diversion of up to 14.5 GL of annual in-stream flows from the Yarramalong Weir represents a significant reduction in in-stream flows and increased potential for impacts on the hydrological dynamics of this section of the river. This is supported by reported declines in exchange between surface flows and groundwater (CSIRO 2008, Chapter 2) in this river section. The floodplain adjacent to the Middle river section is also the most highly developed and modified of the three river sections sampled, with a greater relative proportion of cropping, offstream storages and groundwater bores and a lower proportion of natural vegetation than either the Upper or Lower river sections (Chapter 2).

Shallow alluvial aquifers have been found to play a critical role in supporting phreatophytic vegetation and buffering riparian ecosystems through periods of low precipitation and soil moisture availability (Elmore *et al.* 2006a). Reduced buffering capacity, contributing to more extreme ‘effective drought’ conditions (Elmore *et al.* 2006a), may drive a higher rate of species decline in this section of the study area, relative to the Upper and, in some cases, Lower river sections. Surrounding land use has been found to play a large role in riparian community condition (e.g. Tabacchi *et al.* 1996, Aguiar and Ferreira 2005), and has significant potential to influence both native species diversity (Moffatt and McLachlan 2004, Martin *et al.* 2006) and the presence and dispersion of alien plant species (Moffatt and McLachlan 2004).

The significant interaction between river section and grazing treatments for total species richness and diversity may also be important, although lack of adequate replication for grazed sites in the Lower river section indicates that this result should be treated cautiously. Significant grazing-precipitation interaction reported in other studies (e.g. Burke *et al.* 1998, Allen-Diaz and Jackson 2000, Lunt *et al.* 2007a), especially at higher grazing intensities, suggests that interactions between grazing and resource availability are potentially important factors in the stability of ecosystems. This is supported by evidence of significant interaction between grazing and flooding on the condition of riverine and riparian ecosystems along the Murrumbidgee River, southern NSW (Roberston and Rowling 2002), and also in the lippia-invaded Gwydir wetlands, northern NSW (Berney *et al.* 2010, Price *et al.* 2010a). These findings indicate the potential for cross-scale interactions and for complex ecosystem responses in floodplain landscapes.

3.4.2 Patterns in functional group diversity

Differences in richness, abundance and diversity patterns in a number of functional response groups across river section treatments further support an interpretation of reduced hydrological and ecological function (or increased dysfunction; Chapter 1) along the Middle river section of the study area. While the functional groups examined are not mutually exclusive (i.e. species in this dataset are members of several functional response groups), and responses are likely to be the result of multiple interacting influences in this landscape, significant response in these groups (specifically, C3, C4, forb and perennial species groups) supports the proposition that this more degraded (less dynamic) ecological state is likely to be predominantly associated with more intense effective drought conditions due to a low level of accessible moisture resources.

Both C3 and C4 species are significantly impacted by severe dehydration. Species with C3 physiology are physiologically vulnerable to low moisture availability (Yu *et al.* 2005). In these species, stomatal closure to prevent dehydration constrains photosynthesis, resulting in poor fitness (i.e. low growth and reproductive effort) (Lee and Bazzaz 1986, Moreno *et al.* 2008). While C4 species are physiologically adapted to avoid moisture stress and inherently more water-use efficient than C3 species (Yu *et al.* 2005), they have also been found to suffer metabolic failure under extreme soil moisture deficit (Kalapos *et al.* 1996, Ripley *et al.* 2007).

Regardless of metabolic pathway, many perennial species in water-stressed environments develop deep-root systems (Owensby *et al.* 1999, Huang and Fu 2000), and persistence of these species in drought periods may depend on continued access to stored subsoil moisture (Gibbens and Lenz 2001, Veneklaas and Poot 2003). In alkali meadows in California USA, such species have been found to be highly responsive to the presence of shallow groundwater, which effectively buffers them against drought and soil moisture deficit (Elmore *et al.* 2006a). However, over a period of 16 years, groundwater decline below the average maximum effective rooting depth of perennial groundcover species in that system (2.5 m) induced a threshold response in the abundance of those species; cover remained high at groundwater depths above 2.5 m, despite variation in precipitation, but was significantly reduced where depths exceeded 2.5 m (Elmore *et al.* 2006a).

More complex interactions are also reported in some systems. Persistence of perennial species in drought periods may be dependent on access to moisture redistributed by deep-rooted species through hydraulic lift from deeper soil layers (Dawson 1993a,b,c, Hawkins *et al.* 2009). In the study reported by Elmore *et al.* (2006a), significantly slower response to groundwater decline was evident where there was greater cover of deep-rooted shrubs, which acted to minimise the impact on associated herbaceous species. However, Ludwig *et al.* (2004a, b) report that increased competition for scarce surface soil moisture from hydraulic lift by *Acacia tortilis* in East Africa results in no net benefit for undercanopy herbaceous species.

Diverse groups, such as forbs, are likely to encompass both short-lived and perennial species, and C3 and C4 species, and hence a wide range of adaptations and water-use efficiencies. Ephemeral forbs, in particular, are adapted to rapid response (germination, establishment, growth, reproduction) to improved environmental conditions, and are therefore likely to be adversely affected by low resource conditions (Tsialtas *et al.* 2001, Lechmere-Oertel *et al.* 2005). However, species not specifically adapted to the hydrological extremes experienced in dryland floodplain environments (Colloff *et al.* 2010, Colloff and Baldwin 2010) may be more susceptible to changes in landscape hydrology which increase effective drought conditions and act to filter poorly adapted species (Chapin *et al.* 1993).

While reduced hydrological function is likely to be a primary factor in the observed responses in this study, significant interaction between land use and river section treatments was also apparent in a number functional group patterns, indicating the potential for complex ecological responses to interactions between grazing and resource availability as previously recognised in a number of studies (e.g. Burke *et al.* 1998, Allen-Diaz and Jackson 2000, Lunt *et al.* 2007a). This is reinforced by the finding that within-patch grazing had limited independent impact on functional group responses in this study. However, significant functional group response is generally associated with gradients in grazing intensity (e.g. Lavorel *et al.* 1997, McIntyre and

Lavorel 2001); these were not tested in this study, which was concerned only with broad responses to the presence or absence of grazing *per se*.

The lack of significant response in the abundance and diversity of clonal species in this study is counter to previous studies which generally classify such species in the 'increaser' response group under high grazing pressure (Lavorel *et al.* 1997, McIntyre and Lavorel 2001, Vesk and Westoby 2001). Such species are well adapted to surviving grazing damage, possessing multiple resprouting buds (Liu *et al.* 2007, Benot *et al.* 2010), and frequently increase under grazing pressure as other more susceptible species decline (Liu *et al.* 2007). They are also well adapted to flooding disturbance, and are typically common in floodplain environments, where interactions between flooding and grazing can frequently contribute to their proliferation (Benot *et al.* 2010, Berney *et al.* 2010). Limited response in this group under current climatic conditions may be an indication that this group is not well-buffered against drought or that responses in this group occur at a finer scale than was tested in this study, as suggested above.

3.4.3 Patterns in the dominant weed, lippia

Lippia, a clonal deep-rooted perennial C3 species, was the most frequent and abundant species recorded in this study. As predicted, frequency was a poor measure for such a pervasive (over-dispersed) species (Morrison *et al.* 1995*)*. Cover estimates (1 m^2 quadrats) indicated a high level of variability between samples, especially where grazing was present; however, distinct patterns were not evident at the scales investigated in this study (landscape-and patch-scale). Patterns in lippia abundance have been noted in response to different grazing and flooding intensities (Price *et al.* 2010a), small-scale variations in microclimatic conditions due to topography (Arias *et al.* 2005) and interactions with other species (Taylor and Ganf 2005).

The prevalence of lippia in the study landscape has been linked to high stocking rates and grazing pressure (both current and historical) in these woodlands (QMDC 2005). Lippia establishment and abundance is promoted by flooding, in combination with disturbances such as grazing which provide areas of bare soil and reduce competition from existing groundcover species (Price *et al.* 2011). Grazing exclusion enables recovery of native groundcover (QMDC 2005) and results in a decline in lippia cover in many, but not all, instances (pers. obs.). However, this study indicates that, despite this, lippia persists and is a dominant component of native ecosystems in this landscape independent of current land management.

Lippia has been present in the study landscape for over 80 years, having been first recorded at Tummaville (in the Upper river section of this study, between Talgai and Yarramalong weirs) in 1927 (Lucy *et al.* 1995, Earl 2003). Prior to the 1950s and '60s and development for cropping, the predominant land use on the floodplain was livestock grazing (Chapter 2). Interactions between flooding and high intensity grazing are likely to have promoted the spread and establishment of lippia, particularly within riparian areas (Stokes *et al.* 2007, Price *et al.* 2010a, 2011, Berney *et al.* 2010). The removal of grazing from many of these areas with the development and intensification of irrigated agriculture has seen a decline in the abundance of lippia in many remnants (e.g. QMDC 2005); however, lippia persists as the most widespread species within floodplain riparian vegetation communities in the Upper Condamine landscape. A soil seedbank germination trial conducted in conjunction with this study (results not presented) indicated that this species has a significant persistent germinable soil seedbank at most sites (22 of 24 sites sampled, and second only to *Einadia* spp. in terms of abundance) in this landscape. This is further supplemented by its ability to propagate from vegetative fragments, which are also spread by floodwaters (Taylor and Ganf 2005), under suitable conditions (MacDonald 2008, Price *et al.* 2011). These factors are indicative of ongoing significant risk to native riparian ecosystems associated with lippia in the Upper Condamine landscape.

While this study was not designed to investigate the ecological impact of lippia, it does report the major contribution by lippia to the similarity of sites within treatments in this study. This suggests a significant homogenizing effect (Reinhart *et al.* 2005, McKinney and La Sorte 2007) on community composition and diversity in the study landscape. This may be particularly associated with reduced diversity of ephemeral herbs (forbs and graminoids) in this landscape, in response to past or current prevalence of lippia in these ecosystems. Forbs contribute significantly to ecosystem biodiversity and provide important inter-tussock groundcover in native perennial grasslands (Tremont and McIntyre 1994, Fensham 1998a). Lippia, a perennial clonal forb with highly plastic growth habits (Taylor and Ganf 2005), is adept at pre-empting space in invaded landscapes (Taylor and Ganf 2005). This species exhibits a densely rooted matting ('phalanx') growth form under suitable growing conditions of high light (Xu *et al.* 2010b) and nutrient (Clech-Goods 2010) availability, in combination with adequate soil moisture (Taylor and Ganf 2005). Where conditions are less suitable, especially where taller-growing perennial tussock grasses are dominant, it tends to grow in an elongated trailing exploratory (‘guerrilla’) form (Taylor and Ganf 2005). Both forms indicate a capacity to pre-empt available space and temporally available resources in invaded landscapes, roles usually occupied by ephemeral species (e.g. Morgan 1998a,b, Rosenthal and Lederbogen 2008) which may consequently be excluded. Long-term persistence of lippia in these landscapes may further exacerbate the decline of ephemeral native species, including forbs, through depletion of persistent seedbanks (Benson and Hartnett 2006, Navarro *et al.* 2006).

3.4.4 Significance and limitations

This study confirms the perception that the Upper Condamine is a lippia-dominated landscape, at least in riparian and active floodplain sections of the catchment. This species has high reproductive capacity and the ability to form an abundant and persistent germinable soil seedbank (Macdonald 2008), as well as effective dispersal, establishment and growth strategies under suitable disturbance and resource availability conditions (Stokes *et al.* 2007, 2008, Price *et al.* 2011), and is unlikely to be readily controlled in these systems. These systems therefore fall into the category of novel ecosystems as defined by Hobbs *et al.* (2006), where altered species composition, due to the effectively irreversible presence of alien species or ‘human agency’, implies new interactions, responses and function in these systems. Hobbs *et al.* (2006, 2009) argue that the management of such systems is therefore more efficiently and effectively directed towards retaining ecological function than in attempting to restore these systems to an original pre-development state, particularly given the limited societal resources and potential trade-offs involved.

In terms of function in these systems, this study identifies significantly different floristic composition and lower response diversity (functional redundancy) in a number of functional response groups in the Middle and, to a lesser extent, the Lower river sections of the Upper Condamine Water Supply Scheme. This coincides with evidence of more highly impacted in-stream flow patterns, more intense water resource use and greater levels of floodplain development reported in Chapter 2.

However, this study was not able to effectively separate either the spatially correlated influence of current hydrological conditions and adjacent land use, or the temporally correlated impact of past land use and altered hydrological regimes, on overall community composition and structure.

Despite this, drought impacts at the time of the study were more intense in the Middle and Lower river sections, with significantly greater response in hydrologically sensitive groups (i.e. C3, C4 and forb species). Species associated with dryland river systems are likely to be variously adapted to the hydrological extremes of both drought and flooding (Colloff and Baldwin 2010), and may display considerable resilience in landscapes which have historically experienced a high degree of stochasticity in these events (Capon 2003). However, the potential for ecological processes to buffer the full impact of these extremes (e.g. Elmore *et al.* 2006a) indicates that susceptible species may also show limited response where stabilizing feedbacks (e.g. hydraulic lift in response to declining soil moisture levels) occur in such systems. Significant decline in these functional groups in this study may be associated with increased sensitivity to rainfall variability due to reduced buffering capacity in parts of the landscape where there has been more extensive groundwater decline (CSIRO 2008, Chapter 2) or which support a relatively low cover of deep-rooted phreatic species (as suggested by Elmore *et al.* 2006a); this is supported by evidence of reduced abundance of perennial herbaceous species in this study, which also corresponds with findings previously reported by Elmore *et al.* (2006a).

While community response in this study varied in relation to longitudinal river sections, the impact of flow regulation on overall ecosystem function is difficult to establish with any certainty in such a highly modified landscape, where the level of hydrological modification and land use intensification are interconnected (Chapter 2). In addition, this study was not designed to test temporal variability associated with patch dynamics (e.g. in response to flooding), the influence of historical landscape legacies, or variability associated with species interactions at finer (within-patch) scales which may be relevant in these dynamic woodland ecosystems (Fay *et al.* 2008).

Similarly, response to differences in lateral connectivity (i.e. between river bank treatments which captured broad hydrological and land use patterns lateral to the main river channel), may also have been confounded by differences in land use development intensity (as indicated in Chapter 2). Patterns associated with lateral flows (and responses associated with disruption to these) may also be more apparent at the local scale at which changes in historical flowpaths (e.g. due to diversion and capture of overland flow and the location of floodplain infrastructure) and interactions between hydrological connectivity and land use intensity are likely to occur. This is supported by evidence of significant interaction between river bank and within-patch land use treatments in many of the responses measured in this study (e.g. multivariate floristic composition; total or native species richness, abundance and diversity; and a number of functional group measures).

Within-remnant land use (i.e. the presence or absence of grazing) had no discernable over-riding impact on total, native or alien richness, abundance or diversity in this study. Grazing at the scale measured in this study was not designed to differentiate between different levels of grazing pressure (often highly influential in terms of vegetation composition responses, e.g. Fuhlendorf *et al.* 2001, Allsopp *et al.* 2007), hence data from sites that were more conservatively grazed may have masked more substantial responses at those which were intensively utilised. Nor did this study account for the previous grazing history (legacy) of sites, which may continue to influence composition (Lunt *et al.* 2007a) at both currently grazed and ungrazed sites. For example, Prober *et al.* (2002b) report a hysteresis effect in previously grazed grassy box woodlands in south-eastern Australia, associated with feedbacks between high soil nutrient levels and annual weed species, which prevents recovery. However, as stated above, significant interactions between grazing and hydrology (in particular, lateral connectivity) were apparent and may be important.

3.5 Conclusions

The overall conclusion from this study is that a number of community patterns in riparian woodland remnants on Upper Condamine floodplain conform to broad-scale longitudinal patterns in hydrology and land use, with significant changes in community structure and response diversity in sites along river sections most significantly impacted by floodplain development and by changes in hydrological conditions (as identified in Chapter 2). Significant patterns in vegetation community composition and structure (overall and functional group richness, abundance and diversity) were especially apparent in groups which were sensitive to drought conditions at the time of sampling, suggesting reduced buffering capacity and increased sensitivity to drought in these sections of the landscape. While this research was not designed to identify causal relationships, the potential involvement of groundwater in conferring resistance/resilience to drought raises questions regarding the impact of groundwater decline and potentially the function of deep-rooted canopy trees in these ecosystems. These issues are explored further in Chapters 4 and 5.

The study also confirms the invaded extent and abundance of the introduced clonal perennial herb, *Phyla canescens* (lippia) within these woodlands (e.g. Voller 1998, McCosker 1996), and supports a general conclusion that the Upper Condamine floodplain is a lippia-invaded landscape (Earl 2003). However, there was no significant pattern in lippia abundance in this landscape in relation to large-scale hydrological connectivity or land use intensity, or within-patch land use, indicating the need for a different approach to investigating lippia responses in these ecosystems (Chapters 5 and 6).

The relative importance of hydrological connectivity in shaping ecosystem response was unable to be identified due to confounding patterns in land use development intensity in this landscape. This study also indicates the importance of cross-scale interactions between hydrological connectivity and land use, and the potential for complex ecosystem responses in highly modified floodplain landscapes. This suggests the need to consider the range of interacting factors, both locally and within the broader landscape context, including land use intensity, hydrology, the presence of invasive weed species, and the role of deep-rooted phreatic species, in order to determine factors driving ecosystem condition and function, and to enable assessment of the resilience and potential future status of these systems (Chapter 5).

Chapter 4 Patterns in canopy tree condition in riparian woodland communities on the Upper Condamine floodplain

4.1 Introduction

Native floodplain ecosystems in production landscapes are subject to significant degradation pressure associated with altered disturbance regimes (Tockner and Stanford 2002). Modification of the hydrological, material and energy flow regimes which define floodplain ecosystem structure and function (Walker and Thoms 1993, King *et al.* 2009) can contribute to reduced resilience to disturbance, and threaten the long-term persistence of native ecosystems (Walker and Meyers 2004, Walker *et al.* 2006). The impacts of disturbance and environmental change on key functional species, such as dominant canopy species in woodland or forest ecosystems, may be of critical importance in understanding the response dynamics of these systems (Walker 1995). This may be particularly true in systems in which these species play a critical functional role on which other species depend (Ebenman and Jonsson 2005). Changes in the condition (health, population structure) of dominant 'controlling' (*sensu* Holling 1992) or 'driver' (*sensu* Walker 1995) species may contribute disproportionately to the rate of ecological change (Ebenman and Jonsson 2005), and be indicative of significant shifts in the structure and function of ecosystems subject to anthropogenic modification (Jones *et al.* 1994, Walker 1995, Peterson *et al.* 1998). Response dynamics in such species may provide a critical indication of ecosystem health and resilience and an important yardstick to sustainable land management for ecosystem service provision (including biodiversity conservation) in highly modified landscapes.

This chapter explores the condition of dominant canopy species in remnant riparian grassy woodland ecosystems on the Upper Condamine floodplain, a highly modified production landscape.

4.1.1 Trees and resilience in grassy woodland ecosystems

Savanna ecosystems exhibit key characteristics of complex adaptive systems (Mills *et al.* 2006, Chapter1). Their structure and productivity are governed by dynamic interactions between climate, soils, and disturbances such as fire and herbivory

(House *et al.* 2003, Beerling and Osborne 2006), operating across temporal and spatial scales (Coughenour and Ellis 1993). Water availability appears to be an important factor controlling the tree: grass ratio in these environments. Coexistence is based on resource partitioning by shallow-rooted herbaceous species and deeper-rooted tree species, with relative rooting depth (and tree separation) increasing with aridity (Schenk and Jackson 2002a,b). The rooting depth of plants has important implications for hydrological balance and carbon and nutrient cycling in ecosystems (Canadell *et al.* 1996); this is particularly the case where species influence ecosystem water balance through hydraulic redistribution, a phenomenon reported in a number of savanna-type ecosystems (e.g. Scholz *et al.* 2002, Ludwig *et al.* 2003, 2004b, Scott *et al.* 2008).

In harsh environments, woody species may contribute to increased community diversity by moderating microclimatic conditions and soil physical and chemical properties, thereby facilitating recruitment and improving the water status, nutrient content, carbon assimilation rates and growth of herbaceous species (Moro *et al.* 1997a,b, Ludwig *et al.* 2004b, Armas and Pugnaire 2005). While community patterns and dynamics are the product of multiple, complex interactions including resource competition (e.g. Ludwig *et al.* 2003, 2004a), facilitative processes such as hydraulic redistribution, ‘nurse’-plant effects and N-fixation are increasingly recognised as critically important processes in plant communities (Callaway 1995, Pugnaire *et al.* 1996). Positive interactions such as these underpin the importance of functional (keystone, foundation, driver) species, particularly in highly variable environments, and highlight the potential risks associated with their loss (or in some cases, introduction).

Forests and woodlands with only one or two foundation species, have limited functional redundancy (Walker 1992, Chapter 1). The loss of such species entails a loss of ecosystem function, and is also likely to lead to rapid and irreversible non-linear shifts in biological diversity, system-wide changes in structure and function (Ebenman and Jonsson 2005) and the emergence of novel forest types (Ebenman and Jonsson 2005, Hobbs *et al.* 2009). However, while there is general understanding that plants contribute to overall ecosystem function through changes to micro-climatic conditions and regulation of resource availability (Facelli and Pickett 1991), the specific role of key plant species in the function and stability of ecosystems has not been widely investigated or reported (Ellison *et al.* 2005). Ellison *et al.* (2005) warn that because such tree species tend to be common, abundant, and large, our responses to their decline are frequently too late and at inappropriate scales. This is compounded by the incremental pattern of decline in such species across a range of temporal and spatial scales, often resulting in a mosaic of increasingly fragmented remnant communities across landscapes (Ellison *et al.* 2005), which is likely to escape attention unless systematically monitored.

4.1.2 Tree condition in modified landscapes

Studies investigating tree decline in dominant species have shown association with a range of often interacting factors, including drought, insect irruptions and intensification of land use (e.g. Fensham 1998b, Reid 1999, Banks 2006, Allen 2007). Dieback responses in eucalypts appear to be driven by fundamental abiotic stressors such as drought (Rice *et al.* 2004, Fensham and Fairfax 2007), and altered disturbance (fire, flooding) regimes (Jurskis 2005a, Wen *et al.* 2009) associated with changed land use cover and management (Wylie *et al.* 1992). While dieback has been noted in larger woodland or forested areas (e.g. Kemmerer *et al.* 2008, Cunningham *et al.* 2010), it is particularly evident in rural landscapes which have been significantly modified and developed for agriculture (Landsberg and Wylie 1988, Wylie *et al.* 1992, 1993). In a survey of rural tree dieback, landholders in Queensland reported poor condition in 67 species (Wylie *et al.* 1992); this was thought to be symptomatic of changes in resource availability associated with land degradation. (e.g. changes in landscape function; Ludwig and Tongway 1995) or altered hydrological processes (e.g. Bramley *et al.* 2003). Alternatively, altered tree condition may be in response to novel environmental factors introduced as a component of current land use. For example, Banks (2006) reported significant impact on tree condition in *Eucalytus populnea* associated with herbicide drift on the intensively farmed Liverpool Plain, northern NSW. Biotic factors, such as root fungi (e.g. Weste and Marks 1987) and chronic insect attack (Landsberg 1990a, Lowman and Heatwole 1992, Clarke and Schedvin 1999), can also play a critical role. However, biotic involvement appears to be generally associated with physiological responses in trees (e.g. production of palatable nutrient-rich epicormic growth, changed chemical signals) to initial (primary) environmental stresses (Lowman and Heatwole 1992, Clarke and Schedvin 1999, Hanks *et al.* 1999).

Changes in tree condition may also actively reinforce land degradation trends through positive feedback loops (Hobbs and Suding 2009). For example, some eucalypt species (e.g. *Eucalyptus nova-anglica*) on the New England tablelands, northern NSW, are subject to high levels of insect defoliation linked to fertilization of non-native 'improved' pastures to improve livestock productivity (Reid 1999, Close and Davidson 2004). Tree responses to defoliation in these species include prolific production of fresh epicormic growth which reinforces further insect attack in a positive feedback loop contributing to declining fitness and increased risk of mortality in individual trees (Lowman and Heatwole 1992), altered population processes in affected species, and landscape change in terms of tree cover and species dominance (Reid 1999). Changes in catchment hydrology associated with broadscale tree clearing in the wheat-sheep belt of southern Australia has resulted in groundwater rise, increasing soil salinity, and tree decline in discharge (frequently floodplain) environments (Jolly *et al.* 1993, Overton *et al.* 2006). The ecological impact of this process is compounded by declining functionality and evapotranspiration in deep-rooted trees in these environments, contributing to further groundwater rise, more widespread salinisation and accelerating tree decline (Thorburn *et al.* 1993).

4.1.3 Riparian tree responses to changes in hydrological connectivity

The function and dynamics of floodplain riparian ecosystems are understood to be largely controlled by hydrological disturbance regimes (Hughes 1997); however, much of this understanding is based on studies of ecological responses in floodplain and riparian ecosystem on perennially flowing streams in humid environments with a long history of human-induced landscape modification (Thoms and Sheldon 2002, Vervoort 2007). Flooding in these systems provides recruitment opportunities for flood-adapted and flood-tolerant tree species, filters out those which are less well adapted to cope with flooding disturbance or inundation, and maintains a stable species dominance regime (Hughes 1997, e.g. Bornette and Amoros 1996, Cowell and Dyer 2002). Hydrological modification (flow regulation) and altered dynamics in these systems contribute to increased diversity of generalist canopy species and woodland systems which are more susceptible to major flood events (e.g. Deiller *et al.* 2001, Cowell and Dyer 2002).

In ephemeral dryland (semi-arid) systems, riparian community responses indicate that native tree species in these systems are adapted to, and often dependent on natural disturbance dynamics and associated levels of resource availability inherent in these systems (e.g. Thorburn and Walker 1994, Stromberg and Patten 1996). In such landscapes, flow regulation and extraction of water resources for agricultural production (irrigation) or urban purposes can result in extreme hydrological stress in affected ecosystems (Horton *et al.* 2001a,b), and changes in the condition and function of individual trees, population processes of dominant species or the structure and function of ecological communities (Rood and Mooney 1990, Scott *et al.* 1999, Lite and Stromberg 2005).

Riparian tree species, even in arid and semi-arid regions, are frequently mesic and highly dependent on access to reliable water sources, including in-stream surface water, soil moisture (supplemented by over-bank flooding), and shallow groundwater (e.g. Mensforth *et al.* 1994, Thorburn and Walker 1994, Stromberg and Patten 1996). Such species tend to be poorly adapted to cope with water deficit, and their health is likely to be closely related to hydrological status (McDowell *et al.* 2008, e.g. Bacon *et al.* 1993, Cooper *et al.* 2003b). Under water deficit conditions due to drought or modified hydrological conditions, trees in these systems may exhibit stress responses ranging from adaptive canopy thinning and minor branch sacrifice, which reduce transpirational demand and conserve hydraulic status (Tyree and Sperry 1988, Rood *et al.* 2000), to irreversible failure (embolism and cavitation) in transporting xylem tissue (Tyree and Ewers 1991, Breda *et al.* 2006, McDowell *et al.* 2008). Changes in critical plant processes (e.g. water uptake, photosynthesis) associated with hydraulic dysfunction may result in secondary impacts associated with carbon starvation. These may include reduced capacity for root growth (Friend *et al.* 1994), and potentially reduced resistance to biotic agents, such as borers, often observed in drought-stressed trees (e.g. Hanks *et al.* 1999).

Native tree species in systems affected by hydrological stress due to regulation and extraction often exhibit major shifts in population dynamics which contribute to altered community dominance, ecological function, and system dynamics (e.g. Merritt and Cooper 2000, Lite and Stromberg 2005). For example, on semi-arid zone rivers in western USA, flow regulation and diversion have dampened hydrological dynamics, reduced flooding and contributed to declining groundwater levels (e.g.

Shafroth *et al.* 2000, Stromberg *et al.* 2007a). Reported impacts include declining health and altered population processes in dominant native riparian woodland canopy species such as *Populus fremontii* and *Salix gooddingii*, and an increase in establishment and replacement opportunities for more drought-tolerant tree species such as the alien *Tamarix ramosissima* (e.g. Stromberg *et al.* 1996, Smith *et al.* 1998, Lite and Stromberg 2005).

River red gum responses to hydrological change

The river red gum *Eucalyptus camaldulensis* (Dehnh.) is one of the most widespread species in Australia, occurring along many inland river systems including those of the Murray-Darling (Wen *et al.* 2009). Declining crown condition in *E. camaldulensis* communities in the southern Murray-Darling Basin has been reported in association with increasing landscape salinisation, reduced flooding due to river regulation and surface water extraction, and persistent drought on the Murray and Murrumbidgee floodplains (Cunningham *et al.* 2010, Wen *et al.* 2009). Poor tree health is reported particularly where flooding is restricted in conjunction with high salinity levels (e.g. Chowilla floodplain, Jolly *et al.* 1993, 1996, Overton *et al.* 2006). Despite moderate to high salinity tolerance (Bell 1999, Benyon *et al.* 1999), *E. camaldulensis* exhibits reduced leaf area and loss of hydraulic function with increasing salinity levels above 8 dSm^{-1} (Benyon *et al.*1999), and water stress (physiological drought) at levels over 40 dSm^{-1} (Mensforth *et al.* 1994). Flooding plays a vital role in maintaining tree health by flushing salt from surface soils where it has accumulated due to rising groundwater tables (Slavich *et al.* 1996, Akeroyd *et al.* 1998, Bramley *et al.* 2003).

Conversely, river regulation resulting in a higher frequency of unseasonal flows and flooding has contributed to widespread tree decline where *E. camaldulensis* forests occur in conjunction with effluent wetlands in this system (e.g. the Barmah-Millewa forest) (Chong and Ladson 2003). This may be associated with a number of environmental factors, including duration of inundation, moisture stress following inundation, and salinity. Bren (1987) reported that *E. camaldulensis* was able to survive extended continuous inundation for 24 to 48 months before showing signs of stress. Kozlowski (1997) suggests that, while flood-tolerant species such as E. *camaldulensis* exhibit a range of morphological and physiological adaptations to waterlogging, extended periods of inundation may lead to reduced drought-tolerance post-flooding due to changes in root function, mycorrhizal associations, and the root:shoot ratio. Combinations of inundation and salinity may also have greater impact on growth and survival than either stress alone (Kozlowski 1997). Seedlings of *E. camaldulensis* have been reported to be relatively tolerant of waterlogging conditions, but less so of waterlogging where waters are highly saline (van der Moezel *et al.* 1989).

Declining condition in *E. camaldulensis* due to water deficit has been reported in sections of the Murray Darling Basin over the recent prolonged drought and associated period of low-flow conditions (Doody and Overton 2009). Poor condition of *E. camaldulensis* on the Macquarie River and sections of the Macquarie Marshes in central New South Wales has also been linked to disconnection of the floodplain from the river due to a proliferation of earthen banks and levees associated with floodplain farming which limit the extent of overbank flooding (Steinfeld and Kingsford 2008), although it is not clear from this study whether this response was primarily due to water deficit or the involvement of salinisation processes.

Access to groundwater during drought periods is likely to be an important factor for *E. camaldulensis*, which is well-recognised as a facultative phreatophyte (Mensforth *et al.* 1994, Thorburn and Walker 1994); however, the impact of groundwater decline on this species has not been widely investigated. Groundwater decline due to extended drought or lack of flooding was thought to be a significant factor in increased mortality in a 40-year old *E. camaldulensis* plantation on the Murrumbidgee floodplain (Horner *et al.* 2009). This study reported significantly increased mortality where groundwater depths exceeded 12–15 m. Rooting depth is an adaptive characteristic in young *E. camaldulensis*, as indicated by rapid root extension in saplings in response to falling subsoil moisture levels (Calder *et al.* 1997); however, in other species, trees which have matured during periods of high water availability may be less tolerant of water stress than those which have survived water deficit as they were growing, indicating a limit to further adaptation in older trees (Shafroth *et al.* 2000, Kozlowski and Pallardy 2002).

4.1.4 Tree responses to grazing in riparian ecosystems

Few studies have considered the additional impacts associated with within-remnant management (e.g. grazing) in riparian ecosystems (Robertson and Rowling 2000, Jansen and Robertson 2001), and none have specifically addressed the impact of grazing on the condition of riparian trees. Studies conducted in riparian woodlands are largely focused on the impact of grazing on canopy species population processes, and specifically recruitment (e.g. Meeson *et al.* 2002). Seedling survival is also frequently constrained by grazing (Fischer *et al.* 2009) leading to recruitment failure and skewed populations of canopy species in grazed landscapes (e.g. Pettit 2002).

4.1.5 Study overview

Community patterns, including floristic composition, community structure and response diversity, in riparian woodland remnants on Upper Condamine floodplain, reported in Chapter 3, conform to broad-scale longitudinal patterns in hydrology and land use in this highly modified landscape. Significant response was apparent in functional groups which were sensitive to drought, suggesting reduced buffering capacity and increased sensitivity to drought particularly in the most altered Middle river section of the landscape. The question was raised regarding links between groundwater decline and the function of deep-rooted phreatic canopy trees (*Eucalyptus camaldulensis/E. tereticornis*) in these ecosystems. High levels of dieback, reported in this species complex, are potentially indicative of major ecological change and altered processes in this landscape.

While light to moderate eucalypt dieback was reported earlier on the Darling Downs (Wylie *et al.* 1992), significant decline in the condition of the floodplain ‘river frontage’ forests occurred following the onset of prolonged drought in 1991 (Voller 1998). Voller (1998) identified changes in the riverine landscape over the 60 years since 1935, including increased evidence of dieback symptoms in canopy species, limited regeneration and growth of dominant eucalypt species, and increased prevalence of the native subcanopy species *Acacia stenophylla*. Several potential causes (salinity, psyllids, herbivory) of tree decline in Upper Condamine riparian woodlands were investigated by Voller and Eddie (1995), but the study failed to identify any primary cause (Voller 1998). Observed changes were attributed to a combination of factors, including repeated defoliation by high common brushtail possum (*Trichosurus vulpecula*) numbers, combined with insect attack and cockatoo damage, drought severity, weed competition, grazing, and intensification of land use (Voller 1998). Salinity was not found to be closely associated with the observed decline (Voller 1998), and hydrological factors (e.g. altered flow and flood regimes, groundwater changes) and broader landscape patterns were not considered.

As indicated above, studies in other river systems have found significant impacts on the condition and survival of mature canopy trees in riparian woodlands associated with rivers subject to altered hydrological regimes due to impoundment, flow regulation or diversion. This study asks whether current perceptions regarding the impact of modified hydrological regimes on the response dynamics of dominant tree species in remnant floodplain riparian ecosystems are applicable in this highly modified production landscape. It uses the stratified design implemented in Chapter 3 to investigate whether there are significant effects of differences in longitudinal and lateral connectivity (i.e. between river section and between river bank treatments, respectively) and within-remnant land use (i.e. the presence or absence of livestock grazing) on the size, condition and frequency of *Eucalyptus camaldulensis/E. tereticornis* and *Acacia stenophylla* in remnant riparian woodland ecosystems on the Upper Condamine floodplain.

4.2 Methods

A general description and map of the study area is provided in Chapter 2.

4.2.1 Survey design

This study used the same survey design and sites as the study reported in Chapter 3. In summary, a total of 24 sites was sampled within remnant *Eucalyptus camaldulensis/E. tereticornis*-dominant riparian woodlands along the regulated section of the Condamine River between January and April in the summer of 2004–2005. The study area was stratified *a priori* by (i) river section (Upper, Middle, Lower); (ii) river bank (Left, Right), and (iii) within-remnant land use (Grazed, Ungrazed by domestic livestock). River sections corresponded to the scale of stream-flow data, with end-points of each longitudinal section marked by the location of streamflow gauging stations at in-stream weirs: Talgai to Yarramalong (Upper), Yarramalong to Lemon Tree (Middle), Lemon Tree to Cecil Plains Weir (Lower). River bank treatments investigated differences in factors influencing lateral overland flow parameters on opposite sides of the main river channel. Within-remnant land use captured broad patch-scale management impacts on vegetation composition and condition.

Sample site locations are as described in Chapter 3.

4.2.2 Data collection

Site details

Site condition and woodland structural composition details are reported in Chapter 3.

Woody species composition

At each site, seedling count data were collected for woody species rooted within the modified 1,000 m^2 nested squares quadrat system, as reported in Chapter 3.

Tree health

The size, dispersion, canopy condition and reproductive condition of the four mature canopy trees (one per quadrant) nearest to the centre point of the 1,000 m^2 quadrat were recorded.

Measurements included distance from the quadrat centre point, tree girth (D_{130}: circumference at 130 cm height converted to diameter), and tree height. Canopy projected foliage cover (%) of trees was estimated visually. Canopy condition was scored on a 4-point scale (0: no evidence to 3: considerable evidence; after Le Brocque and Buckney 1995) for dieback (as indicated by tip death, epicormic growth), pathology (yellowing or necrosis of leaves), arboreal herbivory (damaged leaves), and cockatoo damage (tip pruning), where ‘tip’ refers to new growth at the outer canopy edge and ‘tip pruning’ was quantified on the basis of the quantity of ‘tip litter’ (pruned tips) on the ground. Reproductive condition was scored using the same 4-point scale for abundance of buds, flowers and fruit. The number of mistletoe on trees, and the number of standing stags (size classes: >50 cm D_{130}, 20-50 cm D_{130}, <20 cm D_{130}) within the sampling quadrat was also recorded.

Measures indicative of tree condition (Table 4.1) were recorded for each tree, including foliage index (FI: estimated proportion remaining of entire canopy) and percentage tree remaining (PTR, a measure of structural integrity). Canopy thinning and loss of major branches resulted in lower estimates for FI and PTR (Banks 2006).

Table 4.1 Definitions for (a) tree health parameters, including (b) categories used to assess crown structure, and (c) categories to assess the position of crown dieback, used in assessments of tree health in mature *Eucalyptus camaldulensis/E. tereticornis* in Upper Condamine riparian woodlands.

(a) Tree health parameters (after Wylie *et al.* 1992, 1993 and Banks 2006).

Variable	**Code**	**Data type**	**Definition**
Foliage Index (FI) (%)	FI	%	percent leaf biomass present relative to healthy reference tree (full crown)
Percent tree remaining (PTR) (%)	PTR	%	percent woody architecture remaining: from 100% (perfect habit) to 10% (trunk only)
Crown structure (CS)	CS	categorical	4 categories(b) describing the states of the foliage in the dominant proportion of the tree crown
Crown Dieback (CD)	CD	categorical	4 categories(c) describing the position of dieback in the crown and the pattern of foliage loss
Foliage colour	-	ordinal	4 categories describing the severity of foliage necrosis (browning) or chlorosis (yellowing): 4-point scale (0: no evidence to 3: considerable evidence)
Foliage growth pattern		categorical	% of canopy for 4 types of foliage growth: tip growth, normal growth, epicormic growth (primary branches), epicormic growth (stem)
Dropped branches	-	binary	absence (1) or presence (2) – indicative of recent structural damage
Tree size	D130	ratio	tree size, as a surrogate measure of age
Mistletoe	-	ratio	number of mistletoe
Herbivory (insect, arboreal herbivores)	-	ordinal	4 categories describing the severity of arboreal herbivory/damage: 4-point scale (0: no evidence to 3: considerable evidence)
Cockatoo/corella damage		ordinal	4 categories describing the extent of tip-pruning activity: 4-point scale (0: no evidence to 3: considerable evidence)

(b) Crown structure (CS) categories (as in Banks 2006)

Crown Structure category	*Definition*
1	Primary crown – typical form of a healthy tree in its class
2	Secondary crown – developed from epicormic shoots ≥50cm
3	Recent epicormic growth ≤50cm – along the trunk and main branches
4	Apparently dead crown

(c) Crown dieback (CD) categories (as in Banks 2006)

Crown Dieback category	*Position of dieback/foliage loss*
1	One side of the tree
2	Lower canopy
3	Progressing from the top of the tree and tips of branches
4	No pattern

4.2.3 Data manipulation

Tree density and health

Tree density was calculated using the point-centred quarter (PCQ) method (Cottam and Curtis 1956), based on the distance of measured trees from the centre point of the quadrat. Although Engerman *et al.* (1994) report that this (and other) plotless density estimation methods are prone to bias where distribution is non-random, the PCQ approach provides a quick and simple comparative measure appropriate to the purposes of this study (random dispersion of trees was assumed, based on a lack of evidence of significant clumping or even-dispersion) (e.g. Debski *et al.* 2000).

Average Foliage Index (AFI) and mean Percentage Tree Remaining (mean PTR) were calculated from Foliage Index (FI) and Percentage Tree Remaining (PTR) estimates of measured trees at each site. Each tree was also categorised according to a health class (HC) system (Wylie *et al.* 1992, Banks 2006), based on its FI and the condition of its woody architecture (Table 4.2). A tree health site index (Weighted Wylie Index or WWI; Wylie *et al.* 1992) was then calculated from the sum of the percentage of trees in each health class (1 to 5) multiplied by a progressive weighting factor to account for increasing levels of dieback severity (i.e. a low WWI indicates good site health):

$$\begin{aligned} \text{WWI} = {} & (\%\text{trees in HC1 x 1}) + (\%\text{trees in HC2 x 2}) + (\%\text{trees in HC3 x 3}) \\ & + (\%\text{trees in HC4 x 4}) + (\%\text{trees in HC5 x 5}) \end{aligned}$$

Table 4.2 Definitions for (a) Health Class, and (b) Weighted Wylie Index (WWI) categories used in assessments of tree health in mature *Eucalyptus camaldulensis/E. tereticornis* in Upper Condamine riparian woodlands (after Wylie *et al.* 1992, 1993 and Banks 2006).

(a) Health Class categories

Health Class	**Definition**
1. very healthy	≥ 95% Foliage Index (FI), vigorous, full habit, few or no stags
2. healthy	75–94% FI, vigorous, few stags, little epicormic growth
3. moderate to severe dieback	30–74% FI, loss of vigour, epicormic regrowth generally present, moderate to poor health
4. very severe dieback	≤ 30% FI, loss of vigour, recent epicormic shoots along trunk and branches from main canopy, stags, very poor condition
5. dead	No foliage, apparently dead crown

(b) Weighted Wylie Index (WWI) categories

WWI range	**Dieback severity category**
0–100	No dieback
101–200	Slight to moderate dieback
201–300	Moderate to severe dieback
301–400	Severe dieback
401–500	Very severe dieback

4.2.4 Statistical analyses

Response variables including health, recruitment and abundance of dominant canopy species (*Eucalyptus camaldulensis/E. tereticornis*, *Acacia stenophylla*) were compared across treatments (river section, river bank, land use) using the 3-way Analysis of Variance (3-way ANOVA) procedure in SPSS version 18.0 for Windows (SPSS Inc. 2009). Prior to analysis, bounded (proportional) data were arcsine transformed, and all data were screened and transformed (either square root or $\log_{10}$), where required, to meet assumptions of normality and homoscedascity (Quinn and Keogh 2002). Where heteroscedastic variances were unable to be corrected for by transformation, no further analysis was undertaken. Where variances were homogeneous (Levene's), 3-way ANOVA was conducted and Tukey's unplanned multiple comparison procedure with Bonferroni adjustment for unequal sample size (Day and Quinn 1989) was used to determine significant difference between treatment pairs in treatments with significant main effects. Where there was significant interaction between river section, river bank and land use treatments, results indicating significant main effect differences were not able to be interpreted (Zar 1999).

Ordinal categorical variables were analysed using non-parametric procedures in SPSS version 18.0 for Windows (SPSS Inc. 2009). The Kruskal-Wallis procedure for *k*-independent samples (Quinn and Keogh 2002) was used to test for significant difference from expected in river section treatments, with *post-hoc* comparisons between pairs of river section treatments conducted using the non-parametric Mann-Whitney U procedure (Day and Quinn 1989). The Mann-Whitney U procedure was used to test for significant differences from expected in riverbank and land use treatments. No test for treatment interactions was undertaken for these variables (Quinn and Keogh 2002).

Spearman's rank correlation procedure in SPSS version 18.0 for Windows (SPSS Inc. 2009) was used to investigate the strength of association between measures or scores for tree dimensions (diameter, height, canopy area and volume, density), canopy growth (new tips, normal growth, epicormic growth on stems and primary branches), reproductive condition (buds, flowers, seed capsules), tree condition (dead tips, foliage colour, dropped branches, Health Class, Foliage Index (FI), Percent Tree Remaining (PTR)), and evidence of interacting species (mistletoe, arboreal herbivory, tip litter).

4.3 Results

4.3.1 Patterns in tree health

Dominant canopy tree species condition varied considerably across the study area in terms of canopy integrity (AFI), structural integrity (PTR), and dieback severity

(WWI) (Table 4.3). There was also considerable variation in the ranges in size (mean D_{130}) and density of mature canopy trees and in the number of dead trees and number of *E. camaldulensis* and *A. stenophylla* seedlings within $1000m^2$ quadrats (Table 4.3).

Table 4.3 Summary data for canopy species response variables. Values are mean and standard error (24 sites); minimum and maximum values are listed for each variable.

Variable	Mean (SE)	Minimum	Maximum
Average Foliage Index (%)	47.6 (4.4)	17.5	86.3
Weighted Wylie Index	327.8 (16.8)	175	475
Mean Percentage Tree Remaining (%)	73.3 (3.7)	30.0	98.8
Mean D_{130} (cm)	69.2 (4.2)	40.6	129.1
Mature tree density (number/ha)	43.3 (3.9)	12.8	99.5
Age structure (number of age classes)	3.0 (0.3)	1	6
Dead trees (number/$1000m^2$)	1.6 (0.3)	0	4
Eucalyptus camaldulensis/E. tereticornis seedling density (number/1000 m^2)	0.6 (0.2)	0	4
Acacia stenophylla seedling density (number/$1000m^2$)	1.4 (0.6)	0	12

There was no significant interaction between river section, riverbank or land use treatments for measures with homogeneous variances (3-way ANOVA, $p > 0.05$; Table 4.4). Heterogeneous variances (Levene's, $p \leq 0.05$) for average foliage index (AFI), density of dead trees and eucalypt seedling density could not be corrected by transformation, and further analysis was not conducted on these variables.

Significant patterns in canopy tree species health indices (WWI, mean PTR) were found across river section treatments (3-way ANOVA, $p \leq 0.05$). Significantly higher levels of dieback (WWI) and lower levels of structural integrity (mean PTR) were found at Middle river section sites than at Lower river section sites, but there was no significant differences in these variables between either of these river sections and the Upper river section sites ($p > 0.05$). There was significantly lower *A. stenophylla* seedling density (acregen) at grazed than ungrazed sites (3-way ANOVA, $p \leq 0.05$; Table 4.4).

There were no significant differences in canopy tree species health indices across land use or river bank treatments or in *A. stenophylla* recruitment across river section or river bank treatments (3-way ANOVA, $p > 0.05$), and no significant patterns for tree density (treedens), tree diameter (mean D_{130}), or age structure of trees ($p > 0.05$, Table 4.4).

Table 4.4 3-way ANOVA results for key woody species attributes by treatments (river section, river bank, land use). Treatment values are means and standard errors (in parentheses). Significant main effects are indicated in bold type; values sharing the same superscript are not significantly different ($p > 0.05$). Interaction values are F statistics with significance indicated in bold type (** $p \leq 0.005$, * $p \leq 0.05$).

	TREATMENTS							**INTERACTIONS**			
	River section (RS)			**River bank (RB)**		**Land use (LU)**		**RS x RB**	**RS x LU**	**RB x LU**	**RS x RB x LU**
	Upper	**Middle**	**Lower**	**Left**	**Right**	**Grazed**	**Not grazed**				
n	8	9	7	10	14	10	14				
AFI[3]	54.7 (7.4)	33.5 (5.5)	58.3 (10.2)	50.9 (8.0)	45.6 (6.1)	44.4 (7.2)	50.3 (6.5)				
WWI[1,2]	**303.1^{ab} (28.1)**	**383.3^{a} (21.7)**	**282.1^{b} (38.1)**	317.5 (31.4)	333.9 (22.9)	345.0 (28.3)	314.3 (24.4)	0.49	0.83	1.26	0.01
meanPTR[1]	**74.4^{ab} (6.9)**	**58.3^{a} (4.4)**	**85.2^{b} (6.3)**	79.0 (5.6)	66.2 (5.2)	72.1 (6.5)	71.1 (5.2)	0.14	0.30	0.18	0.00
treedens	32.3 (5.4)	49.6 (9.1)	50.2 (5.5)	43.1 (8.1)	44.6 (5.0)	39.1 (5.8)	47.5 (6.2)	0.76	0.80	0.04	3.67
meanD$_{130}$	86.8 (7.6)	57.7 (4. 4)	57.9 (4.5)	64.0 (4.2)	69.9 (6.7)	79.6 (7.3)	58.7 (3.8)	0.77	0.20	0.07	0.07
agestruct[4]	2.6 (0.6)	2.7 (0.4)	4.0 (0.5)	3.1 (0.4)	3.0 (0.4)	2.3 (0.2)	3.6 (0.4)				
deaddens[3]	0.5 (0.3)	2.4 (0.5)	2.0 (0.5)	1.5 (0.4)	1.8 (0.4)	1.8 (0.6)	1.6 (0.3)				
eucregen[3]	0.4 (0.3)	0.6 (0.2)	0.4 (0.3)	0.9 (0.2)	0.1 (0.1)	0.4 (0.2)	0.5 (0.2)				
acregen	1.4 (1.4)	0.1 (0.1)	3.7 (1.6)	0.9 (0.6)	2.1 (1.1)	**0.2^{a} (0.2)**	**2.6^{b} (1.1)**	2.91	1.56	4.52	3.02

[1] arcsin transformed; [2] square root transformed; [3] transformation unable to correct for heteroscedascity (unequal variance) in 3-way ANOVA; [4] categorical variable (analysis by Kruskal-Wallis and/or MannWhitney U).

AFI: average foliage index; **WWI:** Weighted Wylie Index; **meanPTR:** mean percent tree remaining; **treedens:** density of mature trees; **meanD130:** mean diameter at 130cm (mature trees); **agestruct:** age structure of trees; **deaddens:** density of dead trees; **eucregen:** number of eucalypt seedlings (1,000 m^2 quadrat); **acregen:** number of *Acacia stenophylla* seedlings (1,000 m^2 quadrat).

4.3.2 Patterns in foliage growth

There were significant differences between river sections for the proportions of normal growth and epicormic growth on tree stems (Kruskal-Wallis, $p \leq 0.05$), but not for new tips or epicormic growth on primary branches ($p > 0.05$; Table 4.5). The proportion of normal growth was least and epicormic growth on stems greatest at Middle section sites (Mann-Whitney U, $p \leq 0.05$), while Upper and Lower section sites did not differ significantly from each other in either case ($p > 0.05$). There was a significantly higher proportion of epicormic growth on stems at right bank sites than at left bank sites ($p \leq 0.05$), while the proportion of new tip growth was significantly lower ($p \leq 0.005$) and the proportion of epicormic growth on primary branches was higher ($p \leq 0.05$) in trees at grazed sites compared with those at ungrazed sites (Table 4.5).

4.3.3 Patterns in canopy condition

Scores for dead tips were significantly greater in trees on the left bank of the river (Mann-Whitney U, $p \leq 0.005$), but did not differ significantly across river section or land use treatments (Kruskal-Wallis or Mann-Whitney U, $p > 0.05$). Trees at Middle section sites were in a significantly higher Health Class, exhibiting more dieback symptoms (Table 4.2a), than those in the Upper or Lower sections (Kruskal-Wallis and Mann-Whitney U, $p \leq 0.005$). There were significant differences between all three river sections in terms of mean scores for dropped branches (Kruskal-Wallis, $p \leq 0.005$), with Middle section trees scoring significantly higher than those in the Upper section (Mann-Whitney U, $p \leq 0.05$) and both significantly higher than Lower section trees (Mann-Whitney U, $p \leq 0.005$). No significant pattern in foliage colour was evident across any of the treatments (Kruskal-Wallis or Mann-Whitney U, $p > 0.05$; Table 4.5).

4.3.4 Patterns in reproductive condition

There were no significant patterns in reproductive condition (abundance of buds, flowers or seed capsules) across river section, riverbank or grazing treatments ($p > 0.05$, Table 4.5).

Table 4.5 Reproductive condition, foliage condition, canopy condition and evidence of species interactions measures by site groupings (river section, river bank, land use). Treatment values are means and standard errors (in parentheses). Significant within-treatment effects are indicated in bold type; values sharing the same superscript are not significantly different ($p > 0.05$).

	River section[1]			**River bank**[2]		**Land use**[2]	
	Upper	**Middle**	**Lower**	**Left**	**Right**	**Grazed**	**Not grazed**
Number of trees	32	36	28	40	56	40	56
Reproductive condition							
Flower buds (score: 0-3)	0.8 (0.2)	0.7 (0.1)	0.8 (0.1)	0.8 (0.1)	0.8 (0.1)	0.7 (0.1)	0.9 (0.1)
Flowers (score: 0-3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Seed capsules (score: 0-3)	1.2 (0.2)	1.5 (0.1)	1.3 (0.2)	1.2 (0.2)	1.5 (0.1)	1.1 (0.2)	1.5 (0.1)
Foliage condition							
New tips (%)	8.9 (1.3)	10.8 (1.9)	16.4 (3.2)	12.3 (1.6)	11.5 (1.9)	**7.6^{a} (1.2)**	**14.8^{b} (2.0)**
Normal growth (%)	**45.3^{a} (7.0)**	**27.7^{b} (5.7)**	**49.1^{a} (6.7)**	46.8 (5.6)	34.8 (5.1)	36.1 (6.2)	42.5 (4.8)
Epicormic growth – primary branches (%)	34.4 (6.1)	35.6 (5.5)	21.9 (4.8)	31.6 (4.7)	30.9 (4.5)	**40.8^{a} (5.5)**	**24.2^{b} (3.6)**
Epicormic growth - stem (%)	**11.4^{a} (4.1)**	**27.6^{b} (5.6)**	**11.5^{a} (4.8)**	**8.6^{a} (3.2)**	**23.8^{b} (4.4)**	15.7 (4.2)	18.7 (4.1)
Foliage colour (score: 0-3)	1.1 (0.0)	1.2 (0.1)	1.1 (0.0)	1.1 (0.0)	1.1 (0.0)	1.1 (0.1)	1.1 (0.0)
Canopy condition							
Dead tips (score: 0-3)	1.4 (0.1)	1.3 (0.1)	1.2 (0.1)	**1.7^{a} (0.1)**	**1.1^{b} (0.1)**	1.3 (0.1)	1.3 (0.1)
Health Class (score: 0-3)	**3.0^{a} (0.2)**	**3.8^{b} (0.2)**	**2.8^{a} (0.3)**	3.2 (0.2)	3.3 (0.2)	3.5 (0.2)	3.1 (0.2)
Dropped branches (score: 0-3)	**1.6^{a} (0.1)**	**1.9^{b} (0.1)**	**0.6^{c} (0.2)**	1.4 (0.1)	1.5 (0.1)	1.6 (0.1)	1.3 (0.1)
Evidence of interacting species							
Mistletoe (count)	0.4 (0.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.2 (0.1)	**0.3^{a} (0.2)**	**0.0^{b} (0.0)**
Arboreal herbivory (score: 0-3)	**0.6^{a} (0.1)**	**0.5^{a} (0.1)**	**1.0^{b} (0.1)**	0.6 (0.1)	0.7 (0.1)	**0.5^{a} (0.1)**	**0.8^{b} (0.1)**
Cockatoo damage (tip litter score: 0-3)	1.0 (0.1)	0.9 (0.1)	1.1 (0.1)	1.0 (0.1)	1.0 (0.1)	1.0 (0.1)	0.9 (0.1)

[1] Kruskal-Wallis (Mann-Whitney U); [2] Mann-Whitney U

4.3.5 Patterns in interacting species

There was a significant difference in mistletoe frequency across land use treatments, with all infested trees occurring at grazed sites (Mann-Whitney U, $p \leq 0.05$; Table 4.5). There were significantly higher levels of arboreal herbivory in trees at ungrazed sites than at grazed sites ($p \leq 0.05$), and also in trees at Lower river section sites than those in either the Upper or Middle sections ($p \leq 0.005$). No significant pattern in tip-pruning scores (as a measure of cockatoo/corella damage) occurred across any of the treatments ($p > 0.05$, Table 4.5).

4.3.6 Correlations between variables

There was a significant correlation between flower bud score and the proportion of new tip growth, and a significant negative correlation between the flower bud and dead tips scores (Spearman's, $p \leq 0.05$; Table 4.6).

Significant association was found between measures of canopy stress and damage (scores for epicormic growth, foliage colour, and tip death) and measures of tree size (tree height, tree diameter; Table 4.6). Percent epicormic growth on primary branches and dead tips score were significantly correlated with tree height and diameter (D_{130}, $p \leq 0.05$), while percent epicormic growth on the main tree stem was negatively correlated with tree height ($p \leq 0.05$). Percent epicormic growth, both on primary branches and the main tree stem, was also significantly correlated with the score for dropped branches ($p \leq 0.005$). Foliage colour score was not significantly correlated with any measured tree attribute ($p > 0.05$), but was significantly correlated with reduced Foliage Index and a higher Health Class index ($p \leq 0.005$, Table 4.6).

Mistletoe abundance was significantly correlated with tree diameter ($p \leq 0.05$), and cockatoo/corella damage (tip litter score) was significantly correlated with tree diameter and tree height ($p \leq 0.05$, Table 4.6). Arboreal herbivory scores were not significantly associated with any of the tree dimension or canopy condition variables measured ($p > 0.05$; Table 4.6).

Table 4.6 Spearman’s correlations between measures of tree health, tree size, reproductive condition, canopy condition and evidence of species interactions. Values are rho with significant correlation indicated in bold type; superscripts indicate $p \leq 0.005$ (**) and $p \leq 0.05$ (*).

	Foliage Index (FI)	Percent tree remaining (PTR)	Tree diameter (D_{130})	Tree height	Flower buds	Seed capsules	New tip growth	Normal foliage growth	Epicormic growth - primary branches	Epicormic growth - stem	Foliage Colour	Tip death	Health Class	Dropped branches	Mistletoe	Arboreal herbivory
Percent tree remaining (PTR)	**0.72****															
Tree diameter (D_{130})	-0.13	-0.16														
Tree height	0.04	0.17	**0.68****													
Flower buds	0.03	-0.02	0.00	0.08												
Seed capsules	0.02	-0.10	-0.03	-0.01	0.09											
New tip growth	**0.29****	**0.29****	-0.13	-0.11	**0.23***	0.11										
Normal foliage growth	**0.65****	**0.58****	**-0.27***	-0.04	-0.01	0.01	**0.23***									
Epicormic growth - primary branches	**-0.29****	-0.18	**0.46****	**0.43****	-0.19	0.03	**-0.31****	**-0.60****								
Epicormic growth - stem	**-0.56****	**-0.60****	0.05	**-0.23***	0.06	-0.02	**-0.27***	**-0.73****	0.11							
Foliage Colour	**-0.41****	-0.06	-0.10	-0.00	-0.11	-0.01	-0.14	-0.05	0.00	0.05						
Tip death	**-0.23***	-0.01	**0.27***	**0.28****	**-0.27***	0.01	-0.03	-0.02	**0.31****	**-0.30****	0.15					
Health Class	**-0.96****	**-0.69****	0.19	0.04	-0.03	-0.06	**-0.26***	**-0.68****	**0.33****	**0.57****	**0.35****	**0.25***				
Dropped branches	**-0.61****	**-0.77****	**0.28***	0.02	0.07	0.13	**-0.27***	**-0.56****	**0.35****	**0.49****	0.10	0.05	**0.59****			
Mistletoe	0.07	-0.10	**0.23***	0.20	0.05	0.06	-0.08	0.08	0.04	-0.05	-0.06	0.00	-0.01	0.14		
Arboreal herbivory	-0.01	0.14	-0.14	-0.02	0.18	-0.02	0.07	0.01	-0.19	0.09	0.02	-0.15	0.01	-0.17	-0.03	
Cockatoo damage	-0.01	-0.03	**0.29***	**0.23***	-0.06	0.12	-0.06	-0.06	0.13	0.08	-0.17	0.01	-0.03	0.08	-0.09	0.02

4.4 Discussion

Significant variation in canopy tree condition was evident between longitudinal river section treatments in this study. Middle river section sites exhibited significantly poorer tree health than sites in the Lower river section, with Upper river section sites intermediate to the other river sections. These patterns correspond to some extent with differences in land and water use intensity patterns across the river sections identified in Chapter 2, which indicated that the Middle river section exhibited more extreme hydrological impacts (greater loss of streamflow during the prevailing drought at the time of sampling, as well as altered seasonality of flows) and a greater level of land use development than either the Upper or, to a lesser extent, the Lower river sections. Evidence of relatively better tree health, but a high density of dead trees, in the Lower river section indicates a more complex response pattern than was evident for floristic composition (Chapter 3), although in this study there was no evidence of significant interaction between treatments in any tree health measure.

No significant patterns in canopy tree condition were evident in relation to river bank treatments, despite major differences in floodplain and catchment width and in land use development on opposing sides of the river (Chapter 2). Higher mean eucalypt seedling densities were recorded on the Left than the Right bank, but low numbers and heterogeneous variance meant that the data for this measure could not to be statistically analysed). Similarly, presence or absence of livestock grazing at this scale did not significantly influence patterns in canopy tree condition, but there were significantly higher numbers of seedlings of *Acacia stenophylla* at ungrazed sites.

4.4.1 Tree condition and hydrological connectivity

Patterns in tree condition in riparian floodplain woodlands are frequently reported to be driven by hydrological parameters and by the dynamics of overbank flooding in particular (Bagstad *et al.* 2006, Wen *et al.* 2009). Evidence of poorest tree health, as indicated by measures of dieback severity (WWI) and structural integrity (PTR), along the more highly modified less dynamic Middle river section of the study area corresponds with this general finding. However, this may be more closely related to the availability of accessible water resources rather than the overall hydrological variability in the system. The combination of negligible in-stream flows in the period preceding sampling (Chapter 2) and longer-term declines in surface-groundwater exchange and groundwater levels (CSIRO 2008, Chapter 2) in this river section indicate reduced availability of moisture resources, especially during drought conditions. Shallow alluvial aquifers have been found to play a critical role in supporting phreatic vegetation and buffering riparian ecosystems through periods of low precipitation and soil moisture availability (Elmore *et al.* 2006a). Reduced buffering capacity in the Middle section, relative to the Upper river section where surface-groundwater exchange remains active (CSIRO 2008), may contribute to more extreme 'effective drought' conditions and increased dieback severity in this section of the study area.

Substantial groundwater level decline is reported in the study area, particularly in the river sections below Yarramalong Weir (the Middle and Lower sections of this study) (CSIRO 2008, Chapter 2). However, the Middle river section supports a greater intensity of water resource infrastructure (water storages, groundwater bores) and use (irrigated cropping) than either the Upper or Lower river sections (Chapter 2). While the rate and extent of groundwater decline are not explored in this chapter (but see Chapter 5), the greater density of groundwater bores in the Middle river section of this study is indicative of relatively higher pressure on available groundwater resources, which may contribute to the poorer tree condition also evident in this section. Groundwater decline is recognised as a driver of dieback and significant decline in phreatic tree species in many riparian ecosystems (Horton *et al.* 2001a, Schume *et al.* 2004, Stromberg *et al.* 2007b). However, its effect on condition and mortality in either *E. camaldulensis* or *E. tereticornis* has not been reported in the scientific literature. *E. camaldulensis* is a facultative phreatophyte, reliant on shallow groundwater when soil moisture reserves are deficient (Thorburn and Walker 1994). It also exhibits preferential use of groundwater over in-stream water sources when these are accessible (Thorburn *et al.* 1994). *E. camaldulensis* is deep-rooting, and (younger) trees are capable of rapid root extension in response to declining subsoil water levels (Calder *et al.* 1997). While a maximum rooting depth of *E. camaldulensis* is not reported, Mensforth *et al.* (1994) report lateral root extension of at least 15m for trees growing adjacent to streams, and Horner *et al.* (2009) report increased mortality in plantation *E. camaldulensis* where groundwater depths exceed 12 to 15 m.

However, significantly better tree health (lower levels of dieback severity and greater structural integrity) in canopy trees on the Lower river section is counter-intuitive; as in the Middle river section, this section of the river, extending to Cecil Plains Weir, is also significantly affected by groundwater decline (CSIRO 2008, DSEWPC 2009). However, despite classification of these as 'highly disconnected' from the alluvial aquifer/groundwater system (i.e. surface flows no longer contribute to alluvial groundwater recharge), they are also termed 'losing' reaches with significant volumes of surface flows 'lost' in transmission (CSIRO 2008). The apparent paradox in tree condition results may be explained by the location of study sites in the Lower portion of the study area, which were (unavoidably) positioned at either end of the river section (Figure 3.1, Chapter 3), hence non-randomly in terms of proximity to weirs. More variable discharge patterns recorded at Lemon Tree Weir over the ten years prior to sampling, while not representative of flow within the full reach due to the confounding influence of the Condamine North Branch project (Chapter 2), indicate a significant pool of water held behind this weir in most months of the year. Similarly, Cecil Plains Weir is a relatively large in-stream structure holding a permanent body of water to ensure supply to the township of Cecil Plains. These two weirs may act to supplement local groundwater levels in their immediate vicinity and for some distance downstream (e.g. Lane and Zinn 1980, Schade *et al.* 2005), and may significantly supplement shallow groundwater in these locations, contributing to the observed 'improvement' in tree health.

The potential influence of weirs on local groundwater levels indicates an unintended, but positive, outcome for the maintenance of tree health in highly modified dryland river systems, providing artificial refugia which enhance ecosystem stability under drought conditions (although further investigation is required to confirm this). This is in contrast to the effect of in-stream weirs and locks in permanently filled systems, such as the River Murray, which act to augment already shallow groundwater levels associated with altered catchment hydrology (Overton *et al.* 2006). Along the Murray River, rising groundwater levels and associated salinisation in surface soils, exacerbated by lack of flooding due to river regulation, result in poor condition and increased mortality in salt-stressed tree species (Slavich *et al.* 1999, Lamontagne *et al.* 2005c), including *E. largiflorens* and *E. camaldulensis*, both common species on the lower Murray floodplains (Lamontagne *et al.* 2005c). Poor tree health is also reported in *E. camaldulensis* flooded woodlands (e.g. the Barmah-Millewa wetlands on the Murray River) where the seasonality of flooding flows and duration of inundation is significantly altered (Bren 1992, Ladson and Chong 2005). By contrast, altered flooding patterns, rising groundwater levels and associated salinisation do not appear to be significant factors in the current study area; natural flows in the Upper Condamine are essentially ephemeral and, although regulated to some degree, supplemented flows mimic natural patterns with higher flows in summer months (Davies *et al.* 2008). In addition, while there has been a significant decline in the magnitude of smaller flood events with hydrological modification in the Condamine-Balonne system (Thoms 2003, Sheldon and Thoms 2006a,b), flooding associated with larger rainfall runoff events still periodically inundates significant areas of the floodplain, including the riparian woodlands associated with the main river channel (Chapter 2). Salinisation is also not a prominent feature on the Upper Condamine floodplain where shallow alluvial groundwater levels are in decline (Chapter 2).

Lack of response to river bank treatments in this study also potentially indicates the lesser importance of overbank flooding in maintaining tree condition in this landscape. A recent study along the Macquarie River (Steinfeld and Kingsford 2008) investigated the impact of floodplain earthworks associated with irrigation development, flood mitigation and erosion control on flood flow paths and river red gum (*E. camaldulensis*) mortality. That study found that river red gum mortality was significantly correlated with the density of earthworks, although this effect was variable across the study area ranging from highly positive to negative (i.e. mortality increased with density in one area, and decreased with increasing density in another), indicating potentially complex, location-specific hydrological patterns and ecological responses (Steinfeld and Kingsford 2008). A number of studies elsewhere have investigated the ecological impact of flood mitigation levees which limit the extent of overbank flooding across adjacent floodplains, and effectively act to alienate or disconnect floodplain ecosystems from overbank flood flows (Gergel *et al.* 2002a, Kang and Stanley 2005). Significant ecological impact has been reported in some disconnected floodplain ecosystems outside levees, including altered plant community structure and functional dynamics (Kang and Stanley 2005), but not others (e.g. Gergel *et al.* 2002a).

4.4.2 Tree condition and land use intensity

Reduced hydrological connectivity also coincides with evidence of higher levels of floodplain development at Middle river section sites. As reported in Chapter 2, this section has greater overall proportions of cropping (irrigated and dryland), water storages and groundwater bores and a lower proportion of native vegetation than either the Upper or Lower river sections. The poor condition of trees on rural lands in southern Queensland has been previously reported by Wylie *et al.* (1992). Based on the results of a regional landholder survey, the study reported dieback in 67 species, of which *E. tereticornis* was identified as one of four 'indicator' species for southern Queensland; dieback was reported on 62% of the 93 properties where this species occurred, and this species was reported as one of the first in many districts to exhibit dieback symptoms. Dieback in *E. camaldulensis* was reported on three of the five properties on which it was present. The study concluded that, while drivers of tree decline varied with locality, landscape modification and land use intensity were dominant factors associated with the incidence of dieback; the study also indicated that trees on floodplain properties exhibited more severe dieback (Wylie *et al.* 1992, Reid 1999). A subsequent study investigated *E. tereticornis* decline in riparian woodlands of the Mary River catchment, south-eastern Queensland, and also found more severe dieback in areas that were most extensively cleared or intensively managed (Wylie *et al.* 1993). In one of the few studies to investigate the impact of surrounding land use on tree condition, Banks (2006) investigated drivers of declining tree condition in dominant eucalypt species on the Liverpool Plains in northern NSW, a highly modified floodplain landscape very similar to that of the Upper Condamine in terms of topography, soil type and current land use (Banks 2006). The study indicated significant impact on the condition of *Eucalyptus populnea* associated with low concentrations of agricultural pesticides dispersed locally on prevailing winds; however, there was no similar response in *E. camaldulensis* (Banks 2006), indicating different levels of susceptibility. It was suggested that poor condition in *E. camaldulensis* was associated with senescence in larger trees, suggesting a natural process due to aging (Banks 2006); however, in the current study, tree condition and tree size measures were only weakly correlated, bringing into question the over-riding importance of age-related processes in this species.

Within-remnant grazing did not significantly impact tree condition in this study. Livestock grazing has been associated with poor tree health, including eventual mortality of mature trees in other studies (e.g. Davidson *et al.* 2007); however, this is frequently linked to grazing intensification and associated pasture improvement (sowing of introduced pasture species including nitrogen-fixing legumes) and soil fertilization (Landsberg and Wylie 1988, Reid 1999, Close and Davidson 2004), factors not directly examined in this study. The grassy understorey of riparian woodlands on the Upper Condamine floodplain comprise predominantly native grass species, with only incidental evidence of introduced pasture grass species (Chapter 3). These areas are generally not fertilised, although elevated nutrients may occur within these remnants as a result of catchment run-off processes, as is frequently reported for riparian ecosystems (Allan *et al.* 1997); localised concentration of nutrients may also occur under shade trees (stock camps) in grazed remnants (Wilson *et al.* 2007, Chapter 6). Despite this, the findings in this study are in agreement with Fensham and Holman (1999) who also found no association between grazing and dieback in unimproved rangeland savanna landscapes in northern Queensland.

4.4.3 Pattern and process in recruitment and survival of canopy species

Eucalypt seedling numbers, where present, were low (0-4 per 1000 m^2 quadrat) across the study area, and tree recruitment patterns were not significantly related to river section treatments; however, there were more *E. camaldulensis/E. tereticornis* seedlings recorded on the Left river bank where there was also greater incidence of previous flooding (evident in higher flood disturbance scores reported in Chapter 3). This is in agreement with studies in which flooding and sediment deposition are reported to be important factors in seedling recruitment for this species (e.g. Pettit and Froend 2001a,b, Di Stefano 2002), while low numbers of recruits may have been due to inhibition of seed production, poor dispersal, or limited seedling establishment and survival in the study area due to recent prolonged drought conditions (Jensen *et al.* 2007, 2008a).

Grazing is also often reported to have significant impacts on eucalypt seedling establishment and survival (e.g. Opperman and Merenlender 2000, Robertson and Rowling 2000, Fischer *et al.* 2009). Post-dispersal seed density in *E. camaldulensis* is significantly reduced by higher levels of seed predation by ants in riparian woodlands grazed by cattle (Meeson *et al.* 2002). No evidence of grazing impacts on eucalypt seedling abundance was found at the scale of investigation conducted in this study; however, reduced cover of trees under 10 m high at grazed sites (Chapter 3) may reflect a history of reduced recruitment or seedling survival at these sites, expressed in current woodland structure but not apparent in more recent recruitment patterns due to extended drought and limited recruitment prior to sampling. Grazing within woodland remnants can have significant impacts on woodland structure, and is frequently associated with limited recruitment, lower survival of seedlings and skewed age (size) distributions in tree populations (e.g. Pettit 2002, Dorrough and Moxham 2005, Lunt *et al.* 2007a).

In contrast to *E. camaldulensis*, there was evidence of greater recruitment in the canopy subdominant species *Acacia stenophylla,* a small tree which is tolerant of salinity, drought, waterlogging and alkaline soils and widespread on inland river systems (Roberts and Marston 2000, CSIRO 2004). There was also evidence of a significant reduction in recruitment of *A. stenophylla* at grazed sites in this study, supporting a report that seedlings and saplings of this species are susceptible to grazing, particularly at higher grazing intensities (Pettit 2002). Unlike *E. camaldulensis,* however, *A. stenophylla* recruitment is reported to be inhibited, rather than facilitated, by flooding (Nicol *et al*. 2007). The relative success of *A. stenophylla*, despite the prevailing drought conditions in this study may be indicative of its potential as a replacement canopy species where there are minimal impacts from grazing livestock, and hydrological or other factors act to constrain the dominance of *E. camaldulensis/E. tereticornis* in riparian communities. However, the study area is also at the limits of this species' distribution (CSIRO 2004) and the factors limiting the extent of this species on the Upper Condamine warrant further investigation.

4.4.4 Species interactions and dominant tree condition

Significant patterns in the abundance or intensity scores for species which have been observed, or are reported elsewhere, to adversely impact dominant tree condition (i.e. mistletoe, arboreal herbivores, but not Cacatuidae species) were found across river section and land use (grazed, ungrazed) treatments. Association between mistletoe occurrence and grazing has not been previously reported and may be an artifact of the limited sampling, as the 12 individuals were recorded in only 3 trees, all of which were within grazed remnants. Norton *et al.* (1995) found the opposite response to grazing, with no mistletoe in remnants subject to grazing, indicating that this relationship requires further investigation in this landscape. However, there was no evidence of a significant correlation between mistletoe abundance and tree condition, in agreement with Ward (2005) who reported no association between mistletoe infestation and canopy dieback in pink gums *Eucalyptus fasciculosa* in the Mount Lofty Ranges, South Australia. Norton *et al.* (1995) indicated that water relations may be an important determinant of mistletoe abundance, with mistletoes sensitive to changes in the water status of host trees. Alternatively, the limited number of trees supporting mistletoe may be a function of low diversity or abundance of small frugivorous birds in these woodlands, important vectors for these hemiparasitic plant species (Norton *et al.* 1995). Open woodland structure is ideal habitat for noisy miners *Manorina melanocephala* (Clarke and Oldland 2007), an aggressive native bird species associated with limited diversity of other small woodland birds (Grey *et al.* 1997, Clarke and Oldland 2007), and a species frequently observed in the study area (pers.obs.). A combination of prolonged drought and limited dispersal may inhibit mistletoe abundance in these woodlands, which may further exacerbate decline in frugivorous vector species such as mistletoe birds *Dicaeum hirundinaceum* (Lavorel *et al.* 1999c, Watson 2002). Indications are that, while mistletoe species are a driver of decline in host tree species in some situations (Reid *et al.* 1994), they also play an important (keystone) role in supporting the diversity of invertebrates and nectarivores (birds, bats) in ecosystems (Watson 2002, Burns 2009). As such, their low frequency and abundance in this landscape is of concern.

Conversely, evidence of herbivory by mammalian or insect folivores in dominant canopy trees was significantly greater at ungrazed than at grazed sites, and also significantly greater in trees at Lower river section sites in this study, but was not significantly correlated with any of the tree dimension or canopy condition variables measured. These results are counter to reports of widespread and significant insect-related dieback in grazed pastures on the New England Tableland, northern NSW (Lowman *et al.* 1987), and also to evidence of greater herbivory in refoliating canopies (i.e. epicormic regrowth) in eucalypts elsewhere (Landsberg 1990b). These results may, however, reflect differences in the relative water status of trees in grazed and ungrazed remnants. Gordon *et al.* (1988) and Munks *et al.* (1996) both report that tree selection in koalas *Phascolarctis cinereus* is significantly influenced by foliage water content, while Norton *et al.* (1995) report significant impacts on tree water status due to compaction of surface roots by grazing livestock, and a number of other studies report significant increases in soil bulk density (Bezkorowajny *et al.* 1993), degraded surface soil structure (Yates *et al.* 2000) and reduced soil water infiltration rates (Yates *et al.* 2000, Bramley *et al.* 2003) associated with trampling by cattle. Lack of significant association between herbivory levels and epicormic regrowth in this study may be associated with low tree water status and limited mobility and uptake of nutrients from surface soils (Sardans and J. Penuelas 2007) or constraints on insect or arboreal marsupial species population processes (Gordon *et al.* 1988, Kerle *et al.* 1992, Munks *et al.* 1996) as a result of drought.

Significant pressure from arboreal marsupial herbivores on riparian canopy species has been reported in the study landscape (Voller and Eddie 1995). Common brushtail possums *Vulpecula trichosurus* and koalas *P. cinereus* are present, in relatively high numbers, in these woodlands. A supplementary long-term (14 year) study, analysed as part of this research (results not reported), compared canopy condition in paired banded (arboreal marsupial folivores excluded) and unbanded *E. camaldulensis/E. tereticornis* trees at four sites on the Upper Condamine floodplain. This trial found no significant difference in canopy condition between banded and unbanded trees, indicating that arboreal herbivory by possums or kolas is not a primary driver of tree decline in this landscape. However, within the control group of trees, there was evidence of unequal usage by these species, and high visitation rates were correlated with poor tree health, indicating that some trees were preferentially utilised. Foliage was analysed for moisture and N content, as well as the presence of a range of secondary phenolic compounds thought to constitute anti-herbivore defense in eucalypts (e.g. Scrivener *et al.* 2004, Moore and Foley 2005). Significant correlation was evident only between intensity of use by koalas or possums and available N, confirming the importance of a protein-rich diet for these species (Martin 1985); no significant association with foliage water content was found. Lack of evidence for the presence of clear chemical defenses in *E. camaldulensis* (also previously noted by Ian Wallis, pers.com.) may be a function of the range of stress gradients to which this species must respond (through selective allocation of limited carbon resources; e.g. Moore *et al.* 2004) in dryland river environments.

No significant patterns in canopy damage caused by sulphur-crested white cockatoo *Cacatua galerita*/little corella *C. sanguinea* were found in this study. Higher levels of use by these species were evident in larger (taller and larger diameter) trees, but were not significantly associated with dieback symptoms. However, significant damage (debarking of branches) was apparent in individual trees and dead trees adjacent to permanent water appeared to be favoured as roost trees, confirming the highly–localised usage patterns reported elsewhere (e.g. Bomford and Sinclair 2002).

4.4.5 Significance and limitations

This study confirms earlier reports on the condition of Upper Condamine floodplain riparian woodlands (e.g. Voller and Eddie 1995, McCosker 1996, Voller 1998) which identified poor condition, recruitment and survival of dominant canopy species, particularly *Eucalyptus camaldulensis/E. tereticornis*, and increases in the distribution and density of the midstorey species *Acacia stenophylla*. However, it also, importantly, quantifies canopy tree condition and begins to identify differences in dieback severity and canopy tree decline across this landscape.

Poorest tree condition, with most severe dieback and reduced structural integrity, in mature trees of the dominant canopy species *E. camaldulensis/E. tereticornis* was associated with the Middle river section, the reach most significantly impacted by floodplain development and by changes in hydrological flows (Chapter 2). This finding conforms to patterns of significantly reduced floristic and functional diversity in this section reported in Chapter 3. Based on the same survey design, it also coincides with evidence of more highly impacted in-stream flow patterns, more intense water resource and land use, and greater levels of disruption to overland flow patterns in this river section, and was similarly subject to confounded spatial and temporal patterns.

In contrast to Chapter 3 however, tree condition was significantly better (i.e. dieback was moderate rather than severe) on the Lower river section. It is suggested that this finding was influenced by study site locations in this river section, which were biased in terms of relative proximity to weirs. Pooling of surface waters behind weirs may contribute to localised saturation of shallow alluvial sediments, extending downslope of weirs; this may be accessible to neighbouring trees, enabling them to maintain condition through drought. The significant difference in tree condition between the

Middle and Lower river sections is potentially indicative of the importance of accessible groundwater in these ecosystems, but is contrary to the finding in Chapter 3 in which there was no significant difference in floristic composition between the Middle and Lower river sections.

Lack of significant pattern in tree condition in response to differences in lateral connectivity between river bank treatments was unexpected, given greater evidence of flooding and a lower incidence of floodplain structures with potential to modify overland flow patterns on the left bank. While this may have been associated with the broad scale of this comparison (i.e. impact may be more apparent at the local-scale), lack of significant difference at this scale may indicate that surface flow dynamics are perhaps not so important to tree condition in this landscape as reported in other systems (e.g. Jolly *et al.* 1996, Cunningham *et al.* 2010). This is potentially indicative of significantly different processes in this landscape, where there is limited salinisation and a positive association between trees and groundwater, compared to riparian equivalents in the southern Murray-Darling Basin (e.g. Jolly *et al.* 1993). By contrast, overbank flooding remains an important driver of *E. camaldulensis/E. tereticornis* population processes, particularly recruitment, as reported elsewhere (Pettit and Froend 2001a,b, Di Stefano 2002, Jensen *et al.* 2007, 2008b). No similar pattern was evident for recruitment in *Acacia stenophylla*, which is not flood-dependent, and points to a significant differential between these two species, which may be relevant under a changing climate and /or changing levels of resource availability in this landscape.

While overbank flooding is a major component of hydrological connectivity, local overland runoff flows, especially the broad unconcentrated flows which occur across low-sloping floodplain areas with poorly defined runoff flowpaths, are also a potentially important component of landscape connectivity (Clement *et al.* 2003). While levees are not a feature of the Upper Condamine floodplain landscape, significant development of on-farm storages and associated earthworks (banks, ditches, irrigation channels) to control overland flow/rainfall runoff and water flow patterns have resulted in highly modified flood flow paths (Knowles-Jackson and McLatchey 2002). The increased density of floodplain storages in the Middle river section of the study area has potential consequences (e.g, reduced soil moisture, reduced infiltration, reduced seed dispersal) for downslope riparian vegetation and riverine systems into which these flows previously drained. The impact of these on riparian ecosystem function requires further investigation.

Lack of significant pattern in relation to within-remnant land use (presence or absence of grazing) is also somewhat unexpected, as grazing has been an important factor in dieback studies elsewhere (e.g. Lowman and Heatwole 1992, Close and Davidson 2004). This is, in part, a function of the relatively 'natural' state of pastures in riparian woodlands in this landscapes (no 'improved 'pasture species, no fertiliser application), and conforms with the findings of Fensham (1998b) in grazed savanna woodlands in central Queensland. However, grazing on heavy clay soil types, such as the Vertisols of the Upper Condamine floodplain, is reported to cause significant compaction, damaging fine surface roots (Sharrow 2007) and altering soil moisture infiltration characteristics (Bramley *et al.* 2003), which is associated with tree decline elsewhere (Yates *et al.* 2000). This damage may be compounded with declining tree health, defoliation, and associated carbon deficit, which also reduce fine-root production (Friend *et al.* 1994). Reduction in the surface area of fine roots limits hydraulic function in trees and constrains processes such as hydraulic redistribution (Liang *et al.* 1999), further limiting surface soil moisture. Grazing is also reported to have significant impacts on canopy tree population recruitment processes, limiting establishment and survival of seedlings (Clarke 2002, Dorrough and Moxham 2005). The lack of interaction between treatments in this study, in contrast to evidence of this in Chapter 3, may be related to the extremely dry conditions at the time of sampling (Lunt *et al.* 2007b). The lack of significant pattern in *E. camaldulensis/E. tereticornis* seedling density in response to grazing is likely also to be an artefact of poor recruitment associated with the extended period since the last significant flood in 1996. This was in contrast to the recruitment patterns in *Acacia stenophylla*, which had relatively high numbers of seedlings and high frequency of occurrence in non-grazed areas.

A critical factor confounding interpretation of eucalypt responses to altered disturbance and resource regimes is the often significant time-lag between cause and measurable effect in such long-lived adaptive species (Breda and Badeau 2008). Trees exhibit adaptive response to environmental stresses (Kozlowski and Pallardy 2002), and may go through periods of decline and recovery, which in eucalypts is facilitated by the ability to reshoot from lignotubers and epicormic buds in the bark.

While the probability of ecological impact from hydrological changes associated with water resources development is generally well-established in riparian woodland systems, very few studies have conducted investigations which reflect both the altered hydrological and agricultural context of riparian ecosystems (Turner *et al.* 2004). River section treatments in this study were designed to pick up gradients in broad hydrological patterns within the study area; however, spatial variation in a number of other land cover and land use elements at this scale confound interpretation based on hydrology alone. Tree condition in remnant woodland communities elsewhere in Australia exhibits a relatively complex response gradient to a range of environmental factors (Landsberg and Wiley 1988, Landsberg 1990a). This study was not designed to test causal relationships or temporal variability associated with resource dynamics (e.g. in response to flooding) or the influence of historical landscape legacies, some of which may be important to current tree condition and many of which may confound interpretation (Landsberg and Wiley 1988).

4.5 Conclusions

The overall conclusions from this study are that tree condition in this landscape conforms to broad-scale patterns in relation to hydrology and land use intensity, with poorer condition at sites along the Middle river section, which is most significantly impacted by floodplain development and associated changes in hydrology. As in Chapter 3, it is likely that response in mature canopy trees is linked to reduced buffering of drought conditions in this part of the landscape. Poor structural integrity and advanced dieback in these phreatic trees is potentially indicative of severe water stress resulting in branch sacrifice and depletion of functional canopy (e.g. Van der Willigan and Pammenter 1998, Rood *et al.* 2000, Rice *et al.* 2004). This stress is likely to be associated with a combination of drought and severe water deficit within the soil profile, in conjunction with declining access to shallow groundwater levels. While this research is essentially correlative and not designed to identify causal relationships, it indicates again the potential importance of groundwater in supporting system function and resilience under drought conditions.

This study also indicates the role of overbank flooding in terms of recruitment of the dominant eucalypt species *E. camaldulensis/E. tereticornis* in this landscape, and potentially identifies a key differential between this species complex and the subdominant canopy species *Acacia stenophylla.* By contrast it indicates that biotic agents, previously thought to be significant drivers of poor tree condition in this landscape, have only localised impact; however, this requires further investigation under non-drought conditions as the level of interaction observed in this study may alter with greater availability of resources. Similarly, the general lack of interaction between tree condition, recruitment and within-remnant land use may be an artifact of the dry conditions at the time of sampling, and requires further investigation.

As in Chapter 3, the relative importance of hydrological connectivity in supporting tree condition and population processes in dominant canopy eucalypts was unable to be identified due to confounding patterns in land use development intensity in this landscape. Important drivers influencing canopy health, and the role of mature eucalypts in these riparian woodlands, are further investigated in Chapter 5.

Chapter 5 Drivers of floristic composition, community structure and condition in riparian woodland communities on the Upper Condamine floodplain

5.1 Introduction

5.1.1 Environmental drivers in riparian ecosystems

Hydrological gradients are significant predictors (drivers) of overall vegetation patterns in riparian ecosystems (Decocq 2002, Capon 2003, 2005, Leyer 2004, 2005). These gradients act in concert with a range of other variables, including small-scale changes in soil texture and nutrient levels (Beauchamp and Stromberg 2008), the presence of community-structuring species such as trees and functional weed species (e.g. Kercher and Zedler 2004, Stromberg *et al.* 2007a,b), and disturbances associated with grazing (Chaneton and Facelli 1991, Cornaglia *et al.* 2009) or fire (Busch and Smith 1993, Busch 1995, Pettit and Naiman 2007), to influence vegetation communities. Changes in hydrological flow regimes with surface flow modification (e.g. regulation or diversion of in-stream surface flows) are associated with reductions in high flows, as well as altered extent and magnitude of flooding and frequency and duration of low- and no-flow periods, and can have significant impacts on riparian ecosystem composition and function (Stromberg *et al.* 2007a). Altered hydrological gradients are also important determinants of condition in riparian tree species, with water stress a key factor in declining canopy health and tree mortality (O'Connor 2001, Cooper *et al.* 2003b, Horner *et al.* 2009). Reinstatement of historical in-stream flow and flood regimes is viewed as the predominant requirement for restoring ecosystem structure and function in riparian communities (e.g. Tiegs *et al.* 2005, Stromberg *et al.* 2007a,b).

By contrast, the impact on remnant floodplain and riparian ecosystems of changes in resource and disturbance gradients associated with adjacent land use development and intensification has been little studied (Northcott *et al.* 2007). In terrestrial environments, land use change has been associated with altered community assembly processes, through ecological filtering of functional traits, resulting in significant changes in species richness, functional diversity and system function (Mayfield *et al.* 2005). In a global meta-analysis, Laliberté *et al.* (2010) found reduced functional redundancy and response diversity, indicating increasing vulnerability to future disturbances (Walker 1992, 1995), in native vegetation communities along land use intensification gradients. In an assessment restricted to studies from the Americas, Flynn *et al.* (2009) found limited response in plant species richness and functional diversity but significant reduction in the cover of large-statured plants with agricultural intensification. Limited studies of the impact of land use development in riparian systems indicate that land and water resource development may act independently and at times indirectly to significantly alter the structure (patch size) and function (dominant species recruitment) of riparian plant communities (Andersen *et al*. 2007, Northcott *et al*. 2007).

In addition to abiotic drivers, novel biotic components within ecosystems, such as alien plant species, are often reported as potential drivers (engineers) of ecosystem change (e.g. Callaway and Maron 2006, Minchinton *et al.* 2006, Richardson *et al.* 2007). For example, diffuse knapweed (*Centaurea diffusa*) significantly suppresses the growth of native species in invaded communities in western USA (Callaway and Aschehoug 2000, Vivanco *et al*. 2004), while significant species loss and structural shifts have been associated with high infestations of *Lantana camara* in tall open forest in southeastern Australia (Gooden *et al.* 2009a,b). Similarly, certain endemic species are identified as keystone elements which contribute disproportionately to the stability or resilience of an ecosystem; change in the abundance or function of such species may trigger significant change in ecosystem structure and dynamics (Mills *et al.* 1993, Fischer and Lindenmayer 2007, Manning and Lindenmayer 2009). However, while the potential for such change to have significant impact on vegetation community structure and function is recognised (Hooper *et al.* 2005, Manning *et al.* 2006, 2009), it has not been widely investigated or reported.

Fragmented riparian communities in highly modified agricultural landscapes are likely to be influenced by both altered hydrological and novel disturbance regimes associated with anthropogenic land use both within remnants (i.e. at highly localised within-patch scales) and in the surrounding landscape (i.e. at broader ‘meta-patch’ scales which incorporate the agricultural matrix *sensu* McIntyre and Hobbs 1999). This study assesses the relative importance of potential environmental drivers of ecosystem structure and condition in riparian woodland remnants embedded in a floodplain production landscape. It compares community responses to hydrological and land use variables, and combinations of these at scales ranging from within-remnant to the broader agricultural landscape surrounding remnants. It also investigates the role of key functional vegetation species in influencing ecosystem pattern in the study systems.

5.1.2 Ecological response to environmental gradients

Environmental gradients and scale

Ecosystem composition, structure and function are, in effect, the outcome of multiple spatial and temporal environmental filters which result in the selection of individuals (thus species, functional groups, communities, ecosystems) with the ability to respond successfully to the various gradients (Lavorel and Garnier 2002). Plants respond individually to a range of inherently small-scale environmental gradients in abiotic (micro-climate, soil) and biotic (identity and abundance of interacting species) factors (Hook and Burke 2000, Reynolds *et al.* 2003). At the local patch scale, vegetation patterns are an amalgam of species responses to heterogeneous patterns in resource availability, current and past disturbances, and resultant community dynamics (Diaz *et al.* 1999). In floodplain communities, these factors are often determined by gradients in hydrology and connectivity (e.g. Leyer 2004), which, in highly modified landscapes, can be significantly influenced by changes in land cover and levels of resource use at larger scales (Andersen *et al.* 2007).

Interactions across scales are often cited as important drivers of regime shifts (e.g. Suding and Hobbs 2009) but are rarely investigated, with most vegetation community research conducted on relatively small (local, short time-frame) scales (Peterson *et al.* 1998, Carpenter 1999), and focused predominantly on within-ecosystem responses to specific disturbance or resource availability gradients (e.g. McIntyre 2001, 2008, Sutton and Morgan 2009). By comparison, habitat suitability modelling in faunal community studies often includes variables relating to the larger-scale landscape context of vegetation communities (habitat) (e.g. Cushman and McGarrigal 2002, Collard 2007, Kath *et al.* 2009).

Multivariate modelling offers an approach by which the composition of ecological communities may be modelled in relation to gradients in a range of environmental (habitat) variables seen *a priori* as potential drivers (predictors) of community responses (e.g. Knutson *et al.* 1999). Such modelling is essentially a correlative approach, rather than proof of cause and effect; however, the results of such studies are frequently interpreted as strong inference of key drivers and possible mechanisms (e.g. Knutson *et al.* 1999, Kath *et al.* 2009). In addition, this exploratory approach can contribute to the generation of hypotheses which can be further investigated through experimentation (Knutson *et al.* 1999). Such studies can form an important part of the iterative process which enables greater understanding, especially of complex systems subject to anthropogenic change (e.g. Collard 2007, Kath *et al.* 2009).

Measuring and interpreting community response

A critical component of such studies is the choice of metrics relevant to the questions being asked. In plant community ecology, significant progress has been made in terms of developing methods which enable species to be grouped into functional response or effect groups, according to specific morphological and physiological traits (e.g. Volaire 2008, Mabry and Fraterrigo 2009) As examples, plants with high specific leaf area (i.e. leaf area per unit dry mass) are reported to be more successful under grazing disturbance (Golodets *et al.* 2009) or higher fertility conditions (Kuhner and Kleyer 2008), but more prone to moisture stress (Fonseca *et al.* 2000); plants with C4 metabolism are generally more successful (and abundant) in environments where temperatures are higher and/or there is limited moisture availability (Sage and McKown 2006); and many leguminous plants influence ecosystem processes by contributing to soil nitrogen levels (Fornara and Tilman 2008). The classification of vegetation species according to functional trait groups enables comparisons of ecological responses to specific drivers across bioregions, which contributes to the development of general hypotheses of ecological processes and responses (e.g. Loreau 2000, Diaz *et al.* 2007, Suding *et al.* 2008). Diversity within functional groups has also been interpreted as a useful metric for investigating emergent properties of ecosystems in response to ecosystem change with altered disturbance regimes. Redundancy is a key concept relating to functional diversity and system resilience; high levels of diversity within functional groups (i.e. redundancy) is interpreted as indicative of a high capacity for response and recovery, (i.e. resilience), while low functional diversity implies limited options and greater risk (Walker 1992, 1995, Laliberte *et al.* 2010).

Many studies report changes, along environmental gradients, in species composition between groups of species which are effectively reciprocal pairs within a functional trait space. For example, historical change along temperature and moisture availability gradients has driven a transition between relevant functional correlates (e.g. C3 and C4 species) in subtropical bioregions (Huang *et al.* 2001, Nelson *et al.* 2004). On a smaller scale, grazing disturbance is reported to drive a shift from taller-growing perennial grasses to low-growing annual herbs along a grazing intensity gradient (Lunt 1997, Lavorel *et al.* 1999a). While significant development of the functional group concept continues to occur in terms of identifying key traits associated with response to particular disturbances, metrics based on group identity are essentially static, measured in terms of increased or decreased absolute (Wohl *et al.* 2004, Flynn *et al.* 2009) or relative (McIntyre *et al.* 2005, Lavorel *et al.* 2008) redundancy. Change in the proportion of richness (relative redundancy) within a functional trait group, while valuable in interpreting the validity of the functional group approach to identifying meaningful trait sets, implies (but doesn't test) an inverse response in its inverse group (e.g. C3 *vs* C4). As such, such response metrics can be difficult to interpret in a dynamic sense as indicators of change, or resistance/resilience, in community function. The relative richness or abundance of functional correlates (i.e. ratio of richness or abundance of one functional correlate to another) potentially provides a dynamic metric by which community response to a relevant environmental gradient can be tested/measured. This novel metric is used, in this study, to test response in community structure (at the functional group level) to environmental change.

5.1.3 This study

The studies reported in Chapters 3 and 4 found that patterns in the floristic composition and condition of riparian woodlands on the Upper Condamine floodplain conformed to some extent with broad hydrological and land use patterns at the scale of river sections. However, this effect was potentially confounded by issues of scale, and the inability to separate hydrological response from response to land use intensity. Interactions between within-remnant land use, river section and river bank treatments indicated the potential for relatively small scale cross-scale interactions between disturbance, resource availability and ecosystem processes. Significant levels of lippia infestation and dominant canopy species dieback were also evident, and may have significant impact on ecological function in these communities (MacDougall and Turkington 2005, Sardans and Penuelas 2007).

This study investigates the relative importance of hydrological and land use drivers as key determinants of community composition and condition in riparian remnants in this highly modified landscape. It asks how floristic and functional group composition and the condition of key dominant species in riparian woodlands respond to various combinations of potential environmental drivers associated with the hydrological and spatial context of woodland remnants at a range of local landscape scales; it also asks about the role of dominant species in these communities. It uses a multivariate modelling approach to test ecosystem responses, and identify key predictors of composition, condition and function variables. It also utilises a new dynamic functional group-based approach to investigate change in community composition in response to disturbance and gradients in levels of available resources.

Hypotheses addressed in this study are:

(i) that floristic and functional group composition and tree condition in riparian woodlands on the Upper Condamine floodplain are best explained by a combination of hydrological and spatial environmental variables capturing land and water use at a range of local scales; and

(ii) that dieback severity and lippia cover are important predictors of floristic composition in riparian woodlands on the Upper Condamine floodplain.

5.2 Methods

5.2.1 Data collection and treatment

Study area, study design and site selection

Study area, design, site locations and site selection details are as reported in Chapter 2. Three additional ‘reference’ sites were included in this study (total of 27 sites); these were external to the river sections defined in Chapters 3 and 4 (one site was located above Talgai Weir, two below Cecil Plains weir; Figure 5.1). These were identified as ‘best-on-offer’ sites where dominant threatening processes were minimised (Low Choy *et al.* 2005, Eyre *et al.* 2006). No sites that could be considered close to reference (pre-development) condition were available in the study area; reference sites outside the study area were not considered appropriate due to the potential for regional differences.

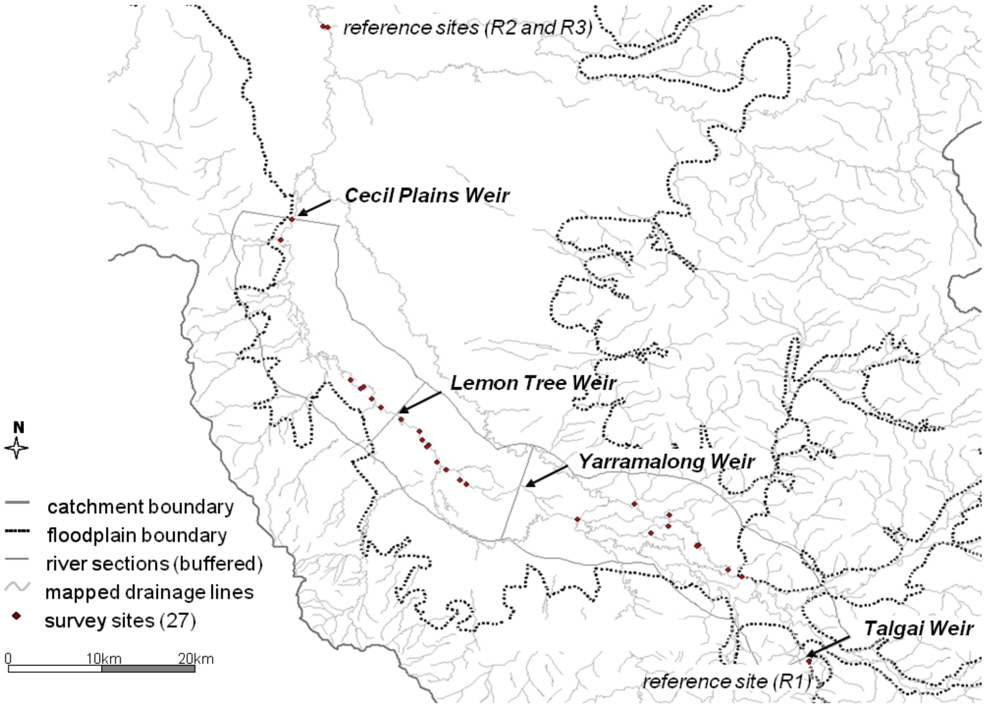


Figure 5.1 Upper Condamine floodplain study area, indicating survey site locations including additional reference 'best on offer' sites (R1-3).

Floristic data collection

Floristic composition was surveyed using a 1000 m^2 nested quadrat frequency sampling method (Le Brocque and Buckney 1997) as reported in Chapter 3. All species recorded were identified, and assigned to functional response groups on the basis of specific physiological, life-cycle, and growth form traits and habitat affinity (wetland, floodplain, terrestrial) (Chapter 3). Mean lippia cover (FPC%) was also recorded (1 m^2 quadrats) as described in Chapter 3. Species richness, abundance (frequency) and diversity measures were derived as reported in Chapter 3.

Functional trait group transitions

Ratios (richness, abundance) for pairs of contrasting variables within functional response groups (Chapter 3) were derived from the vegetation dataset in a novel approach to investigating floristic change. This approach applies the concept of redundancy or functional diversity (Walker 1992, 1995) as a measure of ecosystem resilience, where these ‘functional group transition ratios’ represent potential shifts in functional response capacity within communities. The approach is based on assumptions that (i) functional response group identity is associated with a predictable response to changes in a specific environmental gradient, as outlined in Chapter 3 (Table 3.4); and (ii) ratios between contrasting pairs of functional groups (e.g. C3 and C4 physiology) reflect relative trends in collective species population processes (cumulative abundance) which contribute to relative changes in functional diversity (richness) and provide a dynamic measure of community response.

These functional group richness and abundance transition ratios are used to investigate whether shifts in vegetation community composition are associated with and, by inference, driven by change in relevant environmental variables. If so, this approach may contribute to better understanding of the impact of environmental change within communities, and provide an indication of the key drivers underpinning ecosystem degradation, loss of resilience or potential for regime change. A similar concept is suggested by Cote and Darling (2010) who indicate that selective mortality with disturbance in coral reef communities results in loss of coral species with stress-sensitive life histories and increased dominance (in terms of absolute and relative abundance) of stress-tolerant species. Changes in relative abundance (biomass) of species sorted along trait-based continua have also been used as measures of community response to nutrient and disturbance gradients in grassland ecosystems (Craine *et al.* 2001, Stampfli and Zeiter 2004).

Key functional group transitions investigated in this study (5.1) represent potential compositional or functional shifts in response to resource availability or disturbance gradients associated with broader landscape patterns. For example, a relatively higher ratio of C4 to C3 species might represent a shift to more xeric conditions (Winslow *et al.* 2003, Yu *et al.* 2005).

Table 5.1 Functional group transitions tested in this study.

Transition ratio	**Environmental gradient**	**Reference**
Alien:native	disturbance	Ordonez *et al.* 2010
Short-lived:perennial	disturbance	McIntyre *et al.* 1999b, Bagstad *et al.* 2005
Forb:tussock grass	moisture and/or grazing	Ash and McIvor 1998; Clarke and Davison 2004; McIvor *et al.* 2005
C4:C3	moisture and/or nutrients	Wand *et al.* 1999, Winslow *et al.* 2003, Yu *et al.* 2005
Floodplain:terrestrial	moisture and flooding disturbance	Deiller *et al.* 2001, Stromberg *et al.* 2007a
Wetland:terrestrial	moisture	Stromberg *et al.* 1997, 2007a, Thomas *et al.* 2010
Clonal:non-clonal	flooding disturbance	Lenssen *et al.* 2004a, Insausti and Grimoldi 2006
Clonal:tussock grass	grazing disturbance	Fahrig *et al.* 1994, Rosenthal and Lederbogen 2008

Tree attributes, condition and recruitment

Tree attributes (mature tree density, mature tree diameter), condition (dieback severity, average foliage index, structural integrity, density of dead trees) and recruitment (seedling density) data were recorded for the dominant canopy species complex *Eucalyptus camaldulensis/E. tereticornis* as described in Chapter 4; recruitment data were also recorded for the sub-dominant species *Acacia stenophylla*.

Generation of environmental variables

The landscape context of sites was quantified using spatially arrayed information on land use, land cover, drainage and infrastructure available through the Queensland Government Department of Environment and Resource Management and spatial analysis software (ArcGIS version 9.1, ESRI 2007). Spatial context parameters (e.g. proportions of different land uses, remnant vegetation extent) were measured within areas defined by 500 m, 2000 m and 5000 m buffers centred on each survey site (Figure 5.2) after Collard (2007); these were designed to characterise environmental factors at within-remnant (up to 500 m), adjacent to remnant (up to 2000 m) and local landscape or multi-patch (up to 5000 m) scales. Factors associated with overland flow were captured within buffer segments (approximately quadrants) of the 500 m, 2000 m and 5000 m circular buffers indicated above, defined on one side by the main river channel and, on the other side, by the estimated limit, based on slope, of overland flow to the site (Figure 5.2); these were designed to capture the influence of overland flow. A similar buffer segmentation approach was used by Banks (2006) to investigate the influence of agricultural chemical spray-drift, based on prevailing wind direction, on floodplain tree health. Linear measures (riparian width, distance to river channel, distance to remnant edge, distance to nearest groundwater bore, distance to nearest ring tank) were also calculated for each site. Two response variables, tree health (WWI) and lippia abundance (lippia cover), were also included as explanatory environmental variables; this was to enable the influence of these species as ecosystem dominants to be assessed with respect to their potential roles as ecosystem engineers (Jones *et al.* 1994) or keystone species (Mills *et al.* 1993) in these woodlands.

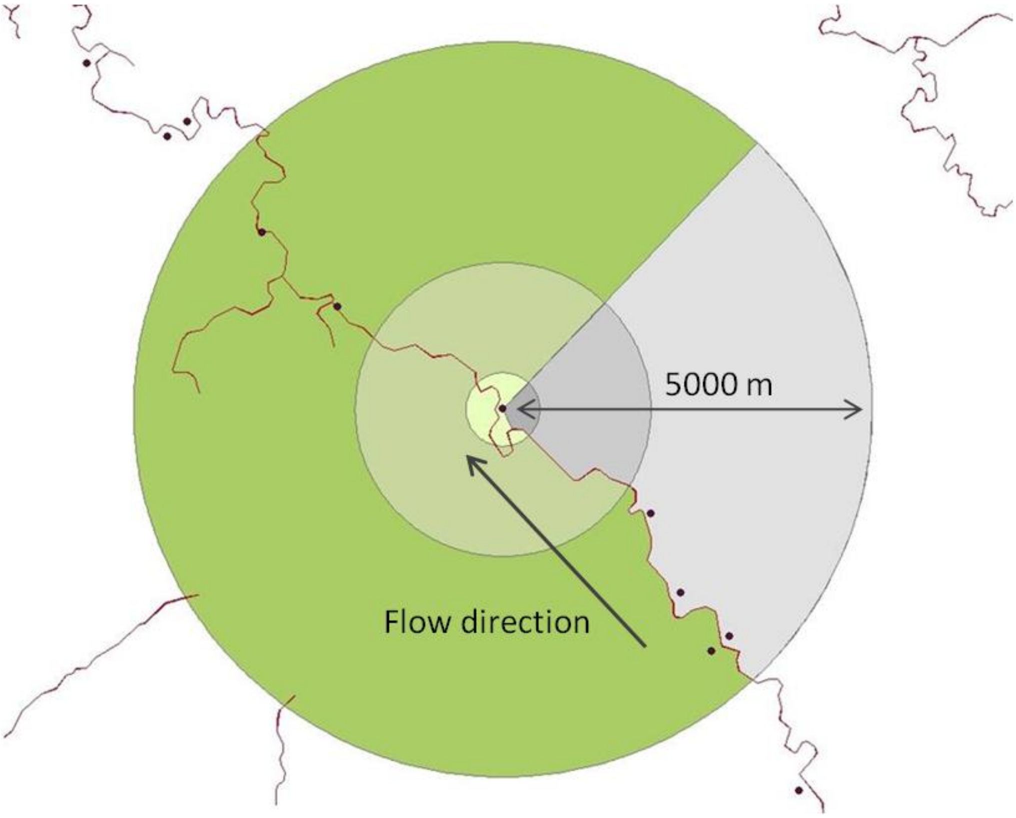


Figure 5.2 Example of buffers and associated quadrants drawn (ArcGIS version 9.1) at 500 m, 2000 m and 5000 m distance from a survey site.

A total of 82 environmental measures was generated (Appendix D). Prior to analysis, measures were sorted into five groups; these were sets of (i) environmental variables capturing hydrological and spatial attributes at all scales (‘Combination’); (ii) hydrological environmental variables (‘Hydrology’); (iii) spatial environmental variables capturing land use (type and intensity) and land cover (native vegetation) (‘Spatial’); (iv) environmental variables capturing hydrological and spatial attributes at the within-remnant scale (‘Patch-scale’); and (v) environmental variables capturing hydrological and spatial attributes at the local-landscape scale (‘Local-scale’). Model sets were reduced to minimum (parsimonious) test sets of potential environmental predictor variables (Table 5.2), using Pearson’s correlation coefficient in SPSS version 18.0 (SPSS Inc. 2009) to identify colinearity within each data set. Where pairs of variables were highly correlated (Pearson’s R ≥ 0.5), only one variable was retained, while preserving as much environmental information as possible in the final test sets (Wintle *et al.* 2003, Kath *et al.* 2009).

Table 5.2 Minimum sets of predictor variables used in Combination, Hydrology, Spatial, Patch-scale and Local-scale (local landscape-scale) models. Values (mean, SE and range) are given in Appendix D.

Variable*	**Dataset**				
	Combination	**Hydrology**	**Spatial**	**Patch-scale**	**Local-scale**
allcropppnUQ2000		x			
bareground	x			x	
cropnatratioUQ2000	x				x
cropnatratioUQ500	x	x			
distdownweir	x	x		x	
distGWprodbore				x	
distriv	x			x	
drainage500	x	x		x	
elevation		x			
grazppn500	x		x	x	
grazppn5000			x		
grazppnUQ500		x			
GW500		x		x	
GW5000	x				x
GWdepth5000	x	x			x
GWirrig5000					x
GWtrend5000	x	x			x
irrigcropppn2000			x		
irrigcropppn500	x		x	x	
irrigcropppn5000	x		x		x
irrigcropppnUQ2000	x				x
irrigcropppnUQ500		x			
irrigcropppnUQ5000		x			
lippiacov	x			x	
north	x		x	x	
remvegppn2000			x		
REremppn2000	x		x		x
REremppnUQ2000	x				x
REremppnUQ500		x			
ringtankppnUQ500				x	
ringtankppnUQ2000	x				x
ripwidthcurrent				x	
treedens	x			x	
WWI	x			x	
Total count	**20**	**12**	**8**	**14**	**10**

* variable descriptions (sampling areas within buffers are indicated as 500, 2000 and 5000, and within quadrants as UQ500, UQ2000 and UQ5000): **allcropppn:** proportion of cropping land use (proportion of sampling area); **bareground:** mean percent cover of bare ground per site (1m x 1m quadrats); **cropnatratio:** dominant land use (ratio all cropping: 'natural' categories); **distdownweir:** distance from the nearest in-stream weir downstream of a site; **distGWprodbore:** distance from the nearest existing registered groundwater irrigation/production bore; **distriv:** distance to main river channel or mapped tributary; **drainage500:** length (km) of river channel/mapped drainage lines within sampling area; **elevation:** elevation (masl); **grazppn:** proportion of grazing land use within sampling area; **GW:** number of existing registered groundwater bores within sampling area; **GWdepth:** average depth to water table (m) (averaged over 2004-5 records) for groundwater monitoring bores within sampling area; **GWirrig:** number of existing registered groundwater irrigation bores within sampling area; **GWtrend:** average trend (rate of decline in m per decade) in water level of groundwater monitoring bores within sampling area; **irrigcropppn:** proportion of irrigated cropping land use within sampling area; **lippiacov:** mean percent cover of lippia per site (1m x 1m quadrats); **north:** northing; **remvegppn:** proportion of mapped remnant vegetation within sampling area; **REppn:** proportion of mapped RE 11.3.25 or 11.3.4 remaining (proportion of preclear extent) within sampling area; **ringtankppn:** proportion of ring tank storage area within sampling area; **ripwidthcurrent:** riparian width; **treedens:** surveyed tree density (#/ha); **WWI:** surveyed dieback severity index (Chapter 4).

These explanatory variables capture a range of disturbance, resource level, connectivity and dominant species gradients in this landscape. These include: flooding disturbance (e.g. bareground, ripwidthcurrent, distriv); within-patch grazing disturbance (e.g. bareground, grazppn500); land cover (e.g. ripwidthcurrent, remvegppn2000, REremppn2000); land use type (e.g. allcropppn, grazppn500); land use intensity (e.g. GW500/5000, irrigcroppn500/2000/5000); resource availability (e.g. elevation, GWdepth5000, GWtrend5000); remnant connectivity (e.g. REremppnUQ500/UQ2000); hydrological connectivity (e.g. distdownweir, drainage500, ringtankppnUQ500/UQ2000); and dominant species function (e.g. lippiacov, treedens, WWI).

5.2.2 Statistical analyses

Multivariate analyses

The PRIMER BIOENV procedure (Clarke and Warwick 2001) was used to identify patterns in environmental variables (Table 5.2) that best matched observed patterns in floristic composition. Each 'sites by variables' matrix was converted to a similarity matrix using Euclidean distance (data normalised and standardised) and compared to Bray-Curtis similarity matrices (species frequency data, standardised) for total floristic composition using the Spearman's rank correlation method (Clarke and Gorley 2001). Sets of independent variables, from individual variables to several (up to 6), from the model test sets (Combination, Hydrology, Spatial, Patch-scale, Local-scale; Table 5.2) were tested to identify the variable or set of variables which best 'explained' (i.e. matched) community patterns (Clarke and Ainsworth 1993).

Univariate analyses

Response variables for functional group species richness and abundance transitions (Table 5.1), and key species (*Eucalyptus camaldulensis*, *Acacia stenophylla* and *Phyla canescens*) parameters were modeled using General Linear Modelling (multiple linear regression) and Bayesian Model Averaging (BMA) procedures (R version 2.9.0: R Development Core Team, 2005 and the BMA package: Raftery *et al.* 2005) with uniform priors (Eicher *et al.* 2007).

Bounded (proportional, percentage) data were arcsine transformed, and all data were screened and transformed (either square-root or $\log_{10}$), where required, to meet assumptions of normality and homoscedascity (Quinn and Keogh 2002). Models were derived from the parsimonious sets of environmental predictor variables (Combination, Hydrology, Spatial, Patch-scale, Local-scale; Table 5.2). A minimum confidence set of models was identified using the Occam's Window approach (Hoeting *et al.* 1999), with models excluded where the maximum posterior model probability (see below) ratio exceeded 20 (Raftery *et al.* 1997, Kath *et al.* 2009).

Models within each confidence set were ranked on the basis of the Bayesian Information Criterion (BIC), which balances goodness-of-fit and model complexity (e.g. Jiao *et al.* 2008), with the minimum (most negative) BIC value signifying the 'quasi-true' or best predictive model (i.e. the most parsimonious model that is closest to the 'truth') as in Burnham and Anderson (2004). Minimum BIC values were compared across the five model sets for each response variable using an information-theoretic approach (Burnham and Anderson 2004, Hobbs and Hilborn 2006) to identify the model best supported by the data (i.e. the 'most informative' set of predictor variables; Table 5.3).

Table 5.3 Grades of evidence used to interpret the strength of the BIC values, BIC differences between models, and posterior effect probabilities for variable effect within Bayesian model averaging (BMA) models (after Raftery 1995)

Minimum BIC	BIC difference (diff)	Probability* (%)	Interpretation
< -10.0	> 10.0	>99	very strong
-10.0 ≤ BIC < -6.0	6.0 < diff ≤ 10.0	95 - 99	strong
-6.0 ≤ BIC < -2.0	2.0 < diff ≤ 6.0	75 - 95	moderate
≥ -2.0	≤ 2. 0	50 - 75	weak

* posterior effect probability

Bayesian model averaging (BMA) was used to investigate the relative weight or importance of test variables within the larger Combination predictor set, identified as the most informative of the five test sets. Model averaging enables robust multi-model inference which accounts for the uncertainty in model selection which is inherent in conventional step-wise regression methods, particularly where a number of possible models perform to a similar level (Raftery 1995, Hoeting *et al.* 1999, Wintle *et al.* 2003). BMA aims instead to identify the best predictive inference from the data by considering all models within the defined confidence set (Raftery *et al.* 1997). Parameter mean and standard deviation, and the posterior effect probability (probability of association), are calculated for each variable across all models, with a probability of 1.00 indicating that a variable is present in 100% of models in the confidence set (interpreted as very strong evidence of effect in the model, Raftery 1995). The regression coefficient (r^2) and posterior model probability (PMP) are calculated for each model; the regression coefficient (r^2) equates to that in conventional step-wise regression methods, and the PMP indicates the percentage of total probability accounted for by an individual model (i.e. a higher PMP indicates a greater level of model certainty) (Hoeting *et al.* 1999).

5.3 Results

A total of 147 vascular plant species was recorded in this survey (Appendix C). Functional group transition ratios ranged from 0.32 – 0.94, a three-fold difference in the relative richness of C4:C3 species, to 0.04 – 1.24, a 31-fold difference in the abundance of wetland:terrestrial species (Table 5.4). There was also considerable variability in dominant species attributes (condition, size, density and cover; Table 5.5) and environmental variables (Appendix D) across the study area.

Table 5.4 Functional group richness and abundance transition ratios for reciprocal pairs of functional groups (V_1 and V_2). Values are means, standard errors (in parentheses) and range (minimum - maximum) of ratios (V_1: V_2) and absolute values (minimum – maximum) for each variable (V_1, V_2).

Variable (V_1:V_2)	Mean (SE)	Ratio (V_1:V_2)		Range (min – max)	
		Min	Max	V_1	V_2
Richness					
alien:native	0.32 (0.03)	0.12	0.75	3 - 19	14 - 35
Shortlived:perennial	0.32 (0.03)	0.13	0.73	4 - 16	13 - 38
Forb:tussock grass	1.07 (0.08)	0.50	2.00	4 - 21	6 - 18
C4:C3	0.61 (0.03)	0.32	0.94	5 - 17	6 - 34
Floodplain:terrestrial	0.69 (0.05)	0.36	1.38	6 - 16	9 - 36
Wetland:terrestrial	0.16 (0.02)	0.04	0.50	1 - 4	9 - 36
Clonal:nonclonal	0.36 (0.02)	0.17	0.70	4 - 14	10 - 39
Clonal:tussock grass	0.86 (0.04)	0.44	1.27	4 - 14	6 - 18
Abundance					
alien:native	0.32 (0.04)	0.12	0.86	9 - 53	28 - 124
Shortlived:perennial	0.25 (0.03)	0.07	0.80	6 - 48	40 - 130
Forb:tussock grass	0.80 (0.05)	0.31	1.47	11 - 56	13 - 70
C4:C3	0.74 (0.06)	0.31	1.49	13 - 59	21 - 97
Floodplain:terrestrial	1.09 (0.11)	0.30	2.64	21 - 58	17 - 109
Wetland:terrestrial	0.24 (0.05)	0.04	1.24	2 - 21	17 - 109
Clonal:nonclonal	0.48 (0.05)	0.22	1.39	14 - 38	23 - 115
Clonal:tussock grass	0.85 (0.06)	0.43	1.88	14 - 38	13 - 70

Table 5.5 Dominant species attributes (condition, size, density and cover). Values are means, standard errors (in parentheses) and range (minimum - maximum).

Dominant species attributes	units	Mean (SE)	Min	Max
AFI	%	46.7 (4.4)	17.5	86.3
WWI	-	327.8 (16.8)	175	475
meanPTR	%	73.3 (3.7)	30.0	98.8
treedens	per ha	43.3 (3.9)	12.8	99.5
mean D_{130}	cm	69.2 (4.2)	40.6	129.1
deadens	per 1000m^2	1.6 (0.3)	0	4
eucregen	per 1000m^2	0.6 (0.2)	1	4
acregen	per 1000m^2	1.4 (0.6)	0	12
lippiacover	%	16.5 (3.0)	0.6	74.0

AFI: average foliage index; **WWI:** dieback severity; **meanPTR:** structural integrity; **treedens:** mature tree density; **meanD130:** mean mature tree diameter; **deadens:** dead tree density; **eucregen:** eucalypt seedling density; **acregen:** *Acacia stenophylla* seedling density; **lippiacover:** mean lippia FPC% (1 m^2 quadrats)

5.3.1 Best predictive model sets

Multivariate models for community composition

Floristic composition was best explained by a multivariate model based on the larger Combination test set (BIOENV, r = 0.45; Table 5.6). This model included a combination of five environmental variables, including mean groundwater depth in 2004–05, mean groundwater trend (m/decade) and the number of existing registered groundwater bores, all within a 5 km radius of survey sites (GWdepth5000, GWtrend5000 and GW5000, respectively), the proportion of the ecosystem type remaining with a 2 km radius of survey sites (REremppn2000), and within-site lippia cover (Table 5.6). The single 'best' variable in this test set was the depth of groundwater (GWdepth5000), which predicted 31% of the variation in community composition (Table 5.6).

Table 5.6 BIOENV models (Combination, Hydrology, Spatial, Patch-scale) for floristic composition based on species frequency data. Spearman correlation values (rho) indicate the strength of the best model using 6 or fewer explanatory variables; the single 'best' variable for each model is also listed. Variable codes are explained in Table 5.2.

Model set	**Spearman correlation (best single)**	**Explanatory variable (best single)**	**Spearman correlation (best set)**	**Explanatory variables (best set)**
Combination	0.31	GWdepth5000	0.45	GWdepth5000, lippia cover, GWtrend5000, REremppn2000, GW5000
Hydrology	0.29	GWdepth5000	0.36	GWdepth5000, GWtrend5000
Spatial	0.35	Grazppn5000	0.40	Grazppn5000, REremppn2000
Patch-scale	0.17	Lippiacover	0.26	lippiacover, ripwidthcurrent, distGWprodbore, drainage500
Local-scale	0.19	REremppn2000	0.34	REremppn2000, GWdepth5000, irrigcroppnUQ2000, GWirrig5000, GWtrend5000

Models based on subsets of predictor variables (i.e. Hydrology, Spatial, Patch-scale, Local-scale) explained a smaller percentage of variation in floristic composition, although models based on the spatial and hydrology variable sets (Spearman's rho = 0.40 and 0.36, respectively; Table 5.6) were more informative that those based only on patch-scale variables (rho = 0.26). Key predictors in these sets were all either included in the best Combination model or highly correlated (Pearson's R > 0.50) with these variables. For example, Grazppn5000, a key predictor in the next best 'Spatial' model, was highly correlated with GWdepth5000 in the Combination set (Pearson's R = -0.88).

Models for functional group transition ratios and dominant species

There were very strong best Combination models for alien:native and short-lived:perennial functional group richness transition ratios (BIC < -10.0, Table 5.7); these were strongly superior to the alternative Hydrology, Spatial, Patch-scale and Local-scale models (BIC difference > 6.0). The Hydrology model for the floodplain:terrestrial richness transition ratio was very strong (BIC < -10.0) and moderately better than the next best Combination model (2.0 < BIC difference ≤ 10.0). The Hydrology models for the wetland:terrestrial and clonal:tussock grass richness transition ratios, and Combination models for the C4:C3 and clonal:nonclonal richness transition ratios were moderately strong (-6.0 ≤ BIC < -2.0), and weakly to moderately stronger than the next best models (2.0 < BIC difference ≤ 10.0). All models for the forb:tussock grass richness transition ratio were null (BIC = 0.0, Table 5.7).

Table 5.7 Bayesian information criteria (BIC) values for the best predictor models within the Combination, Hydrology, Spatial and Patch-scale test variable sets for functional group richness and abundance transition ratios and dominant species attributes. Values are BIC. Very strong models (BIC < -10.0) are indicated in bold type; asterisks indicate the relative strength of the best model over the next best model for each response variable (*** very strong, ** strong, * moderate; as in Table 5.3)

Response variable	Combination	Hydrology	Spatial	Patch-scale	Local-scale
Functional group richness transition ratios					
alien:native	**-18.2****	-4.3	0.0	-7.8	**-10.8**
shortlived:perennial	**-29.6*****	**-10.6**	-4.4	-9.0	**-14.3**
forb:tussock grass	0.0	0.0	0.0	0.0	0.0
C4:C3	-2.4	-2.0	0.0	-1.0	0.0
floodplain:terrestrial	-6.5	**-10.3***	-4.1	-6.5	-5.6
wetland:terrestrial	-2.0	-5.9*	0.0	-1.5	-0.4
clonal:nonclonal	-4.2	-1.8	0.0	-4.2	0.0
clonal:tussock grass	-3.6	-5.5	0.0	0.0	-3.6
Functional group abundance transition ratios					
alien:native	**-19.5***	-5.2	0.0	**-10.7**	**-15.5**
shortlived:perennial	**-22.5*****	-4.7	-4.2	**-10.0**	-4.5
forb:tussock grass	0.0	-0.1	0.0	0.0	-2.1
C4:C3	**-12.7****	-6.4	0.0	-3.5	0.0
floodplain:terrestrial	**-13.9***	-6.3	-6.7	-11.6	-6.2
wetland:terrestrial	-4.7	0. 0	0.0	-4.7	0.0
clonal:nonclonal	-0.7	-0.7	0.0	-0.7	0.0
clonal:tussock grass	0.0	0.0	0.0	0.0	0.0
Dominant species attributes					
AFI	-7.1	-5.7	-7.2	-3.5	-1.4
WWI	-8.2	-5.2	-8.0	-1.1	-0.7
meanPTR	**-21.2****	**-13.3**	-9.6	-7.2	-2.0
treedens	-0.8	-1.6	0.0	-0.8	-5.1
meanD130	**-18.3**	**-12.7**	**-11.1**	**-15.5**	**-17.4**
deaddens	**-24.7***	**-16.4**	**-20.9**	**-12.5**	**-17.1**
eucregen	0.0	0.0	0.0	0.0	0.0
acregen	**-23.1****	**-13.7**	-1.7	-8.5	-3.4
lippiacover	-5.6	**-11.0**	-9.4	-4.5	-7.1

There were very strong best Combination models for alien:native, short-lived:perennial, C4:C3 and floodplain:terrestrial abundance transition ratios (BIC < -10.0, Table 5.7). The short-lived:perennial abundance transition ratio Combination model was very strongly superior to the next best Patch-scale model (BIC difference > 10.0), and the Combination models for the alien:native, C4:C3 and floodplain:terrestrial abundance transition ratios were moderately to strongly better than the next best Hydrology, Spatial, Patch-scale or Local-scale models (2.0 < BIC difference ≤ 10.0). The wetland:terrestrial Combination and Patch-scale models were both moderately strong (-6.0 < BIC ≤ -2.0). The Local-scale model for the forb:tussock grass abundance ratio was at the low range of moderately strong (BIC = -2.1), and all models for clonal:nonclonal and clonal:tussock grass abundance transition ratios were either weak or null (BIC ≥ -2.0, Table 5.7).

Best Combination models were very strong (BIC < -10.0) for mean PTR and acacia regeneration data sets, and were strongly superior to the alternative Hydrology, Spatial, Patch-scale and Local-scale models (6.0 < BIC difference ≤ 10.0, Table 5.7). All models for meanD$_{130}$ and the density of dead trees (deadens) were very strong (BIC < -10.0), but the Combination models were weakly to moderately superior (0.0 < BIC difference ≤ 6.0). There were strong best models for AFI (Spatial) and WWI (Combination) but these were only weakly superior to other next best models (BIC difference ≤ 2.0). There was a very strong Hydrology model for lippia cover, but this was only weakly better than the next best Spatial model; the Combination model for lippia cover was only moderately strong (-6.0 ≤ BIC < -2.0, Table 5.7). The best Local-scale model for tree density was moderately strong (-6.0 ≤ BIC < -2.0), and moderately superior to the next best Hydrology model (2.0 < BIC difference ≤ 6.0). All models for eucalypt recruitment were null (BIC = 0.0, Table 5.7).

5.3.2 *Response models for functional group transition ratios*

Functional group richness transitions

The ‘quasi-true’ (Burnham and Anderson 2004) or best Combination models derived for alien:native and short-lived:perennial richness transition ratios explained a high proportion of variation in the dataset (BMA; r^2 = 84% and 91%, respectively). Models in the minimum confidence set for these response variables (45 and 68 models, respectively) were complex, with several predictor variables present in all models (Table 5.8). Key predictors common to both models were drainage500 (the length of river channel and mapped drainage lines within 500 m), grazppn500 (the proportion of grazing land use within 500 m), and GWtrend5000 (mean trend in groundwater levels within 5000 m), which were all negatively correlated with increased relative richness of alien and short-lived species and/or decreases in the relative richness of native and perennial species. Of the other key predictors in the alien:native richness transition ratio model, distdownweir, irrigcropppnUQ2000 and REremppn2000 were all positively correlated, and GWdepth5000 was negatively correlated, with the relative proportion of alien to native species (Table 5.8). Bareground (mean percent cover of bare ground) and irrigcroppn5000 (the proportion of irrigated cropping land use within 5000 m) were both positive predictors in over 95% of short-lived:perennial richness transition ratio models in the confidence set; lippiacover (the mean percent cover of lippia), north (the GPS northing reading, a surrogate for rainfall and elevation) and land cover within 2000 m upslope (cropnatratioUQ2000, ringtankareaUQ2000) were included in 84-95% of models in the confidence set, and all except ringtankareaUQ2000 were positively correlated with a higher relative proportion of short-lived species.

Models for C4:C3, clonal:non-clonal and clonal:tussock grass richness transition ratios explained up to 42%, 36% and 63%, respectively, of variation in the data (Table 5.8). Lippia cover was the dominant predictor (p = 0.84) of a higher relative proportion of C3 species, while REremppnUQ2000 and irrigcropppn5000 were only moderately strong terms in the C4:C3 richness transition model. The clonal:non-clonal richness transition ratio was best predicted by distance from the nearest downstream weir (p = 0.87) and tree density (p = 0.87), with a higher relative proportion of clonal species closer to the nearest downstream weir and where tree density was higher. Key predictors in the clonal:tussock grass richness transition ratio model were land cover within 2000 m upslope (cropnatratioUQ2000, ringtankareaUQ2000), while lippia cover and REremppnUQ2000 were terms in 69% and 57%, respectively, of models in the confidence set; the clonal:tussock grass richness transition ratio was positively associated with ringtankareaUQ2000 and lippiacover, and negatively correlated with cropnatratioUQ2000 and REremppnUQ2000. The forb:tussock grass richness transition was not predicted by the any of the model terms (Table 5.8).

Table 5.8 Individual models for functional species richness transitions using Bayesian model averaging (BMA). The most consistent model terms (p > 50%) in the confidence sets for each response variable are indicated; numbers in parentheses are the probability of the term being included in a model in the confidence set, and bold type indicates a negative coefficient in the quasi-best model. The number of models in the confidence set (nmodels), and maximum r^2 and posterior model probability (summed PMP) of the top 5 quasi-best models, are listed. Model terms are explained in Appendix D.

Response variable	**p >95%**	**p >75%≤95%**	**p>50%≤75%**	**n_{models}**	**Max r^2 (best 5)**	**∑PMP (best 5)**
Combination models						
Alien:native	distdownweir (1.00), **drainage500 (1.00), grazppn500 (1.00), GWdepth5000 (1.00), GWtrend5000 (1.00),** irrigcropppnUQ2000 (1.00), REremppn2000 (1.00)	-	-	45	0.84	0.32
Shortlived:perennial	bareground (1.00), **drainage500 (1.00), GWtrend5000 (1.00),** irrigcropppn5000 (0.98)	cropnatratioUQ2000 (0.95), north (0.94), lippiacover (0.94), **grazppn500 (0.93), ringtankareaUQ2000 (0.84)**	-	68	0.91	0.26
Forb:tussock grass	-	-	-	33	-	0.37
C4:C3	-	**lippiacover (0.84)**	REremppnUQ2000 (0.62), **irrigcropppn5000 (0.61)**	65	0.42	0.24
Floodplain:terrestrial	-	WWI (0.85)	GWdepth5000 (0.65)	23	0.45	0.22
Wetland:terrestrial		**distdownweir (0.63)**	GWdepth5000 (0.58)	58	0.33	0.24
Clonal:non-clonal	-	**distdownweir (0.87),** treedens (0.87)	-	42	0.36	0.35
Clonal:tussock grass	**cropnatratioUQ2000 (0.98),** ringtankareaUQ2000 (0.93)	-	lippiacover (0.69), **REremppnUQ2000 (0.57)**	99	0.63	0.15
Hydrology models						
Floodplain:terrestrial	GWdepth5000 (1.00)	**REremppnUQ500 (0.95), distdownweir (0.90)**	-	28	0.56	0.46
Wetland:terrestrial	GWdepth5000 (0.99)	**distdownweir (0.94), REremppnUQ500 (0.90)**	-	28	0.47	0.46

Combination models for floodplain:terrestrial and wetland:terrestrial richness transition ratios explained 45% and 33%, respectively, of variation in the dataset (Table 5.8). WWI (dieback severity) and GWdepth5000 were key (positive) predictors in 85% and 65%, respectively, of models within the confidence set for this response variable, while distdownweir (negative) and GWdepth5000 (positive) were key predictors in 63% and 58%, respectively, of wetland: terrestrial richness transition ratio models. The stronger Hydrology models for these response variables (BIC, Table 5.7) included GWdepth5000 in 100% and 99% of models within the respective confidence sets, and REremppnUQ500 and distdownweir in 90-95% of models. In these models, higher floodplain:terrestrial and wetland:terrestrial richness transition ratios were both predicted by greater mean 2004-05 groundwater depths within 5000 m, greater distance for the nearest downstream weir and reduced upslope riparian woodland remnant extent within 500 m (Table 5.8).

Functional group abundance transitions

Combination models explained up to 87% of variation in alien:native, short-lived:perennial and C4:C3 species abundance transition ratios (BMA; r^2 = 87%, 81% and 81%, respectively; Table 5.9). The alien:native species abundance transition ratio was most strongly predicted by a greater proportion of remnant vegetation within 2 km (REremppn2000, p = 0.96), the short-lived:perennial species abundance transition ratio was most strongly predicted by a greater percentage of bare ground and lower dieback severity (WWI); and the C4:C3 species abundance transition ratio was best predicted by lower cover of bare ground and lippia. Floodplain:terrestrial and wetland:terrestrial abundance transition ratio models explained 61% and 41% of variation in the dataset. Dieback severity (WWI) was the most important predictor, present in 100% and 98%, respectively, of models for these response variables, while cropnatratioUQ500 (the ratio of all cropping:‘natural’ land use categories within 500 m upslope) was a strong predictor in 89% of floodplain:terrestrial abundance transition models. Increased floodplain:terrestrial and wetland:terrestrial abundance ratios were associated with greater dieback severity, and floodplain:terrestrial abundance was positively correlated with an increased proportion of cropping upslope (Table 5.9). Models for forb:tussock grass, clonal:non-clonal and clonal:tussock grass abundance transition ratios were not well-predicted by the any of the model terms in the Combination model set (Table 5.9).

Table 5.9 Individual models for functional species abundance transitions using Bayesian model averaging (BMA). The most consistent model terms (p > 50%) in the confidence sets for each response variable are indicated; numbers in parentheses are the probability of the term being included in a model in the confidence set, and bold type indicates a negative coefficient in the quasi-best model. The number of models in the confidence set (nmodels), and maximum r^2 and posterior model probability (summed PMP) of the top 5 quasi-best models, are listed. Model terms are explained in Appendix D.

Response variable	**p >95%**	**p >75%≤95%**	**p >50%≤75%**	$\mathbf{n_{models}}$	**Max r^2 (best 5)**	**∑PMP (best 5)**
alien: native	REppn2000 (0.96)	bareground (0.90), **GWdepth5000 (0.89), GWtrend5000 (0.85),** irrigcropppnUQ2000 (0.82), **drainage500 (0.80),** distdownweir (0.75)	**grazppn500 (0.71), cropnatratioUQ2000 (0.66),** distriv (0.61), **WWI (0.53)**	72	0.87	0.23
Shortlived: perennial	bareground (1.00), **WWI (0.97)**	ringtankppnUQ2000 (0.81)	cropnatratioUQ2000 (0.73), irrigcropppn5000 (0.71), **GWtrend5000 (0.51)**	102	0.81	0.18
Forb: tussock grass	-	-	-	97	-	0.19
C4: C3	**bareground (1.00), lippiacover (0.99)**	GW5000 (0.95), **irrigcropppnUQ2000 (0.93),** grazppn500 (0.92), drainage500 (0.88)	north (0.60), **irrigcropppn5000 (0.58), cropnatratioUQ500 (0.56)**	77	0.81	0.19
Floodplain: terrestrial	WWI (1.00)	cropnatratioUQ500 (0.89)	-	42	0.61	0.37
Wetland: terrestrial	WWI (0.98)	-	-	54	0.41	0.28
Clonal: nonclonal	-	-	**distdownweir (0.64)**	32	0.18	0.38
Clonal: tussock grass	-	-	-	53	-	0.25

5.3.3 Response models for dominant species attributes

The best Combination models for the three tree condition response variables (AFI, WWI, meanPTR) accounted for varying proportions of variation in the dataset (BMA, r^2 = 0.43, 0.63 and 0.84, respectively; Table 5.10). Strong predictors for average foliage index (AFI) were GWdepth5000 (the mean groundwater depth in 2004-5 within 5000 m) and grazppn500 (the proportion of grazing land use within 500 m) ($p > 0.75$), both of which were negatively correlated with response in this variable in the BMA model. Dieback severity (WWI) was very strongly predicted by GWdepth5000 and grazppn500 ($p = 1.00$ and 0.99, respectively), and also strongly predicted by GW5000 (the number of groundwater bores within 5000 m). Strong predictors of the structural integrity of mature trees (meanPTR) included the mean cover of bare ground (bareground), mean 2004-05 groundwater depth within 5000 m (GWdepth5000), rainfall and elevation (north), distance from the nearest downstream weir (distdownstream), the proportion of irrigated cropping land use within 2000 m upslope (irrigcropppnUQ2000), the number of registered groundwater bores within 5000 m (GW5000) and mature tree density (treedens) ($p > 0.75$); structural integrity was positively correlated with north (a surrogate measure of declining average annual rainfall with distance downstream (Chapter 2) and inversely correlated with elevation, $p = -.087$, distance from the nearest downstream weir, the number of groundwater bores and mature tree density, and negatively correlated with increasing bare ground cover, groundwater depth and irrigated cropping upslope (Table 5.10).

Tree size (meanD$_{130}$) models accounted for 74% of variability in the dataset, and consistently included lippiacover (the mean percent cover of lippia) and cropnatratioUQ2000 (the relative proportion of cropping land use and native vegetation within 2000 m upslope) ($p = 1.00$ and 0.98, respectively), while treedens (the density of mature trees) and drainage500 (the length of river channel and mapped drainage lines within 500 m) were strong explanatory variables in 94% and 85% of models in the Combination confidence set for this response variable. There was a positive correlation between mean tree size (meanD$_{130}$) and both lippia cover and drainage500, and negative for mean tree size and cropnatratioUQ2000 and mature tree density. Models for the density of dead trees (deadens) explained 79% of variation in the data, and were best predicted by increases in the proportion of grazing land use within 500 m (grazppn500) and the proportion of irrigated cropping with 5000 m (irrigcropppn5000), and decreased lippia cover. Mean groundwater trend (GWtrend5000) and mean 2004-05 groundwater depth (GWdepth5000) were predictor terms in 86% and 74% of models in the confidence set for this response. Mature tree density was not well-predicted by any of the model terms tested in the combination model set ($p \leq 0.50$), but Local-scale models explained up to 60% of variation with 84% of models in the confidence set containing the predictor term GWdepth5000 and 75% containing ringtankareaUQ2000. Mature tree density in the BMA model was negatively associated with GWdepth5000 and positively associated with ringtankareaUQ2000 (Table 5.10).

Models for *Acacia stenophylla* seedling density (acregen) explained up to 91% of variation in the dataset, but were relatively complex with several model terms consistently present in models ($p \geq 0.98$). Very strong predictor terms with positive coefficients were the length of drainage500, north and WWI (dieback severity); very strong terms with negative coefficients included distriv (distance from the river), irrigcropppnUQ2000 (the proportion of irrigated cropping land use within 2000 m upslope) and REremppnUQ2000 (the proportion of mapped remnant woodland ecosystems within 2000 m upslope). *Eucalyptus camaldulensis/E. tereticornis* seedling density (eucregen) was not well-predicted by any of the model terms tested ($p \leq 0.50$, Table 5.10).

Mean lippia cover (lippiacover) was very strongly predicted by north ($p = 0.99$) in Combination models and elevation ($p = 1.00$) in Hydrology models, which predicted up to 50% and 44% of variation in the dataset (Table 5.10). Spatial models for lippia cover explained 59% of variation in this response variable; the strongest predictor variables in this model set were irrigcropppn2000 (the proportion of irrigated cropping within 2000 m), north, and grazppn5000 (the proportion of grazing land use within 5000 m) ($p = 0.94$, 0.86 and 0.80, respectively). Lippia cover was positively correlated with irrigcropppn2000 and grazppn5000, and negatively correlated with north in these models.

Table 5.10 Individual models for dominant species measures using Bayesian model averaging (BMA). Key model terms ($p > 50\%$) in the confidence sets for each response variable are presented; numbers in parentheses are the posterior effect probability within the confidence set, and bold type indicates a negative coefficient in the BMA model. The number of models in the confidence set (n_{models}), and maximum r^2 and posterior model probability (summed PMP) of the top 5 quasi-best models, are listed. Model terms are explained in Appendix D.

Response variable	$p > 0.95$	$p > 0.75 \leq 0.95$	$p > 0.50 \leq 0.75$	n_{models}	Max r^2 (best 5)	∑PMP (best 5)
Combination models						
Average foliage index (AFI)*	**GWdepth5000 (1.00)**	**grazppn500 (0.89)**	**GW5000 (0.53)**	68	0.47	0.25
Dieback severity (WWI)*	GWdepth5000 (1.00), grazppn500 (0.99)	GW5000 (0.80)	cropnatratioUQ500 (0.53)	63	0.63	0.24
Structural integrity (meanPTR)*	**bareground (1.00), GWdepth5000 (1.00),** north (1.00), distdownweir (0.98)	**irrigcropppnUQ2000 (0.89),** GW5000 (0.88), treedens (0.83)	**ringtankareaUQ2000 (0.53)**	56	0.84	0.31
Mature tree density (treedens)**	-	-	-	46	0.20	0.31
Mean mature tree diameter (mean D_{130})	lippiacover (1.00), **cropnatratioUQ2000 (0.98)**	**treedens (0.94),** drainage500 (0.85)	-	58	0.74	0.27
Dead tree density (deadens)*	grazppn500 (1.00), **lippiacover (0.99),** irrigcropppn5000 (0.97)	GWtrend5000 (0.86)	GWdepth5000 (0.74)	35	0.79	0.36
Eucalypt seedling density (eucregen)	-	-	-	66	-	0.23
Acacia stenophylla seedling density (acregen)	**distriv (1.00),** drainage500 (1.00), **irrgcropppnUQ2000 (1.00),** north (1.00), **REremppn2000 (1.00),** WWI (0.98)	**REremppnUQ2000 (0.92),** irrigcropppn5000 (0.88), **treedens (0.87)**	grazppn500 (0.66), GWdepth5000 (0.59)	65	0.91	0.23
Mean lippia cover (lippiacover)***	**north (0.99)**	-	irrigcropppnUQ2000 (0.74), **ringtankareaUQ2000 (0.53)**	75	0.50	0.19
Alternative models						
treedens$_{Loc}$		**GWdepth5000 (0.84),** ringtankareaUQ2000 (0.75)	**GWtrend5000 (0.65), cropnatratioUQ2000 (0.63), irrigcroppn5000 (0.55)**	54	0.60	0.33
lippiacover$_{Hyd}$	elevation (1.00)	-	-	21	0.44	0.51
lippiacover$_{Spat}$	-	irrigcropppn2000 (0.94), **north (0.86),** grazppn5000 (0.80)	**irrigcropppn5000 (0.57)**	38	0.59	0.40

* Modelling conducted on the model set excluding WWI as response and predictor terms are not independent (Chapter 4); ** Modelling conducted on the model set excluding treedens as a predictor term; *** Modelling conducted on the model set excluding lippiacov as a predictor term.

5.4 Discussion

Multiple environmental drivers of change operate to influence floristic composition, tree condition, and abundance of dominant species in riparian woodland remnants on the highly modified Upper Condamine floodplain, reflecting the complexity of change that has occurred in conjunction with land and water resource development in this landscape. These drivers include both hydrological and spatial (land use and land cover) variables, operating across spatial scales, from a within-remnant patch scale to a meta-patch (multiple remnant, local landscape) scale. This study also indicates that, while hydrological drivers are important predictors of a number of community responses, they act in conjunction with a range of novel disturbances associated with land use type and intensity on Upper Condamine floodplain.

Few response variables in this study were best explained by models based only on hydrological variables; these were floodplain:terrestrial and wetland:terrestrial richness transitions and lippia cover. Other responses were at least as well or better explained by models based on combinations of hydrological and land use/land cover (spatial) variables, and included environmental influences at a range of local landscape scales. A number of strong predictor variables in these response models integrated both hydrological connectivity and land use/land cover (e.g. land use proportions in the upslope quadrant). A small number of published studies suggest the likelihood that both hydrology and surrounding land use are likely to influence riparian woodland community composition and function (e.g. Gergel *et al.* 2002b, Andersen *et al*. 2007, Freeman *et al.* 2007); however, few have specifically tested this (e.g. Aguiar and Ferreira 2005). These papers predict or report significant interaction between hydrology, land use and land cover, as generally indicated in this study.

This study also indicates the significant role played by species interactions, particularly those with dominant functional species. Lippia cover and canopy species tree health (i.e. dieback severity), while responsive to abiotic gradients, were also significant predictors in models for floristic composition and community structure in this study.

5.4.1 Floristic composition (frequency) and functional group transitions

A combination of hydrological and spatial environmental variables explained 45% of variation in overall floristic composition (frequency) in the survey dataset, with the most informative variable being groundwater depth (GWdepth5000). While essentially a hydrological variable and dependent on hydrological connectivity between in stream flow and the shallow alluvial aquifer, groundwater depth in this landscape is also, in many respects, a measure of land use intensity given the chronic groundwater decline experienced since the development of irrigated agriculture on the Upper Condamine floodplain (Chapter 2). This is also the case for the mean decadal groundwater trend (GWtrend5000) and the density of groundwater bores (GW5000) within 5000 m of survey sites, which were also important predictors of overall floristic composition; other key predictors were the non-hydrological variables, lippia cover (lippiacover) and the riparian woodland remnant proportion in and adjacent to surveyed remnants (REremppn2000). By comparison, the model based on hydrological variables only, explained considerably less (36%) of this variation. It is evident that a combination of key hydrological and spatial (land use/cover) variables, as well as the presence of a dominant invasive alien species, was strongly associated with observed floristic composition at the time of sampling in this landscape. The interpretation of multiple environmental drivers of community diversity in this landscape is further supported by significant changes along functional group species richness and abundance transition gradients in response to a number of abiotic and biotic environmental factors.

The transition models used in this study confirm, to some extent, previous findings that different functional response groups are associated with different environmental gradients. For example, alien:native and short-lived:perennial richness gradients were associated with general levels of disturbance, including grazing (McIntyre and Lavorel 2001) and associated degradation (Holm *et al.* 2003). However, most response gradients (i.e. transitions) in species richness and abundance in this study were associated with combinations of, rather than single, environmental variables, supporting the contention that there are complex interacting drivers of ecosystem condition in highly modified floodplain landscapes (Schroder 2006). The exceptions to this were changes in the relative richness of wetland and floodplain species groups compared to habitat-generalist (terrestrial) species groups, which, as in other studies (e.g. Turner *et al.* 2004, Lite *et al.* 2005), were best explained by landscape hydrology; in this study, this included including groundwater depth, flow-related propagule dispersal (REremppnUQ500) and proximity to the nearest downstream weir. On the other hand, the abundance ratios for these functional transitions were more strongly associated with tree health (i.e. dieback severity), supporting a proposition that, while deep-rooted trees operate effectively as intermediaries between groundwater and shallow-rooted herbaceous vegetation (Ludwig *et al.* 2004a, Elmore *et al.* 2003, 2006a), this function may be compromised by declining groundwater depths (Elmore *et al.* 2003, 2006a) and reduced hydraulic function of trees.

5.4.2 Dominant species responses

Dominant tree condition responses

Measures of tree condition were all best explained by combinations of hydrological and spatial (land use, land cover) variables. Canopy health and dieback severity were both strongly predicted by factors associated with patch-scale land use (e.g. grazing within 500 m of sites) and land use intensity at the larger meta-patch scale (e.g. groundwater depth and the density of groundwater bores within 5000 m of sites); both were most strongly predicted by the mean 2004–05 groundwater depth, which ranged from 9.1 to 19.6 m across the 27 sites in this study. Poorer tree condition (i.e. lower AFI and higher WWI) was predicted by deeper groundwater levels and greater numbers of groundwater bores at the meta-patch scale.

Groundwater decline is a pervasive feature of the developed Upper Condamine floodplain, particularly in shallow alluvial aquifers associated with the main Condamine river channel and its tributaries (Chapter 2), and, as in other similar situations (e.g. Stromberg *et al.* 1996, Elmore *et al.* 2003), is potentially an important driver of ecosystem condition in these water-dependent woodlands. Previous studies indicate that there is likely to be an accessible groundwater depth threshold around 15 m for *Eucalyptus camaldulensis*, a facultative phreatophyte dependent on access to shallow groundwater during periods of surface soil moisture deficit (Mensforth *et al.* 1994, Thorburn and Walker 1994). Mensforth *et al.* (1994) report maximum root extension (though lateral) for *E. camaldulensis* of 15 m, and Horner *et al.* (2009) report increased mortality in a densely planted self-thinning *E. camaldulensis* plantation with groundwater decline from 12 to 15 m during recent prolonged drought. The range of groundwater depths associated with survey sites in this study (9.1 to 19.6 m) straddles this potential threshold; groundwater decline which decouples tree roots from accessible moisture resources may contribute to significant decline in the health of trees, particularly during extended drought conditions when surface soil moisture levels are depleted, as indicated by increasing dieback severity with greater depth to groundwater in this study. The strong association between tree health and patch-scale grazing in this landscape, where there is limited pasture improvement or fertilization (as discussed in Chapter 4), is potentially associated with a detrimental impact of livestock on soil condition (degradation of surface soil structure, localised redistribution of soil nutrients) resulting in poor surface root function, reduced soil water infiltration rates and changes in microclimatic conditions at the soil surface, as reported in other studies (Yates *et al.* 2000, Bartley *et al.* 2006, Davidson *et al.* 2007). If the case, such impact would further contribute to effective drought conditions experienced by trees.

Changes in the structural integrity (woody architecture) of trees (meanPTR), while connected with a broader set of environmental variables, are also strongly associated with soil moisture and other accessible water resources. Tyree and Sperry (1988) interpret ‘branch sacrifice’ as a drought adaptation, hence loss of tree branches may in part be a natural occurrence in dominant riparian trees in semi-arid regions; however, loss of major branches is also indicative of significant physiological impact (embolism, xylem cavitation) in response to severe water deficit, and has been associated with declining groundwater levels in riparian woodlands of arid-zone river systems in North America (Tyree and Sperry 1988, Horton *et al.* 2001a,b, Rood *et al.* 2000).

The importance of groundwater depth to mature tree health has been reported in *Banksia/Eucalyptus* woodlands at Cooljarloo, south-western Western Australia, subject to seasonal drought in combination with mining resulting in periodic groundwater drawdown below rooting depth (Froend and Loomes 2007). Other studies have associated eucalypt dieback predominantly with increased land use intensity (e.g. Wylie *et al.* 1992), including pasture ‘improvement’ (introduced pasture species, high levels of artificial fertilisation; Davidson *et al.* 2007) and high levels of agricultural chemicals, particularly herbicides, in cropping areas (e.g. Banks

2006). Riparian eucalypts along the River Murray, including *E. camaldulensis*, exhibit significant dieback in response to rising groundwater levels and soil salinisation, which is exacerbated by lack of flooding due to river regulation (e.g. Wylie *et al.* 1993, Jolly *et al.* 1993, 1996, 2008, Overton *et al.* 2006). Recovery in tree condition has been observed with reduced salinity levels where environmental flows are managed to create overbank flooding and flush salts from surface soils (Holland *et al.* 2009, Overton *et al.* 2010). There has been no published research into altered tree condition in riparian eucalypts, including *E. camaldulensis*, in areas where groundwater levels have declined to the extent reported in this study. In contrast, dieback in phreatic riparian species (e.g. *Salix* and *Populus* spp.) in semi-arid and arid regions in North America is reported to be strongly linked to declining groundwater levels (e.g. Horton *et al.* 2001b, Naumberg *et al.* 2005). These species show evidence of hydraulic stress and dieback symptoms with a decline in groundwater to depths greater than 2.5 to 3 m during periods of critical soil water deficit (Horton *et al.* 2001b).

Froend and Loomes (2007) suggest that, in addition to groundwater depth, the magnitude and rate of water table decline are important factors impacting on the condition of phreatic vegetation. The rate of groundwater decline was not a major component of models for tree health in this study, with the exception of the density of dead trees, indicating that it may be important in some locations. There is an extended legacy of groundwater drawdown in this landscape and the magnitude of groundwater decline has continued to increase over the record period (Chapter 2). Maximum rates of groundwater decline associated with survey sites in this study were 1.8 m per decade (0.2 $m.yr^{-1}$), which is low compared with Froend and Loomes' (2007) prediction that rates exceeding 0.75 $m.yr^{-1}$ result in increased risk of impact on associated vegetation.

Recruitment responses of canopy species

Eucalypt recruitment (eucregen) was not associated with any of the environmental factors tested in this study. However, previous studies have indicated the influence of past land use, livestock grazing, distance to mature trees and cover of exotic annual vegetation for eucalypt regeneration in grassy woodland ecosystems (Dorrough and Moxham 2005). Regeneration in *Eucalyptus camaldulensis* is significantly associated with flooding or rainfall events following canopy seed release, which peaks over summer in the southern Murray-Darling Basin (Jensen *et al.* 2008a). Seed release volumes are reported to be sensitive to tree condition, with water-stressed trees on the Chowilla floodplain, lower Murray River, releasing up to nine times less seed than healthy trees at the same location (5–915 seeds m^{-2} and 605–52,685m^{-2}, respectively) during summer 2004–05. Limited seed release in drought periods or from trees in poor condition (Jensen *et al.* 2008a) may be exacerbated by interactions with grazing intensity which facilitate higher rates of seed predation by foraging ants in this species (Meeson *et al.* 2002), although Jensen *et al.* (2008a) suggests that seedling establishment is unlikely to be limited by seed availability or viability. Germination in *E. camaldulensis* requires water either from local rainfall or flooding, and, while seeds germinate readily along high-water strandlines, survival can be limited where soil moisture levels decline rapidly (Jensen *et al.* 2008a). Highly clumped seedling and sapling patterns on the Murray River floodplain at Banrock Station, South Australia, indicate episodic recruitment and opportunistic survival in this species in response to the high temporal and spatial variability of suitable conditions (George *et al.* 2005). These findings suggest that limited evidence of recruitment in the current study is likely to be predominantly related to the prolonged drought experienced in the years prior to sampling.

Conversely, recruitment of *Acacia stenophylla* (river cooba) is not apparently constrained to the same extent by lack of flooding or drought conditions. The greater incidence of *Acacia* seedlings (and also greater overall *A. stenophylla* frequency) close to the river channel and where there was a higher density of drainage channels emphasises this species' apparent reliance on riverine processes which, though not defined, has been reported previously (Kingsford 2000, Doody *et al.* 2009). Recruitment of *Acacia stenophylla* in this study was higher where dieback severity in eucalypt species was greatest and mature tree density was least, suggesting a possible response to competitive release (Mueller *et al.* 2005, Fensham and Fairfax 2003, 2007) in this sub-dominant species.

Dominant weed responses

Lippia abundance was not well-predicted, except by surrogate measures for long-term average precipitation (elevation, latitude), and a lesser association with grazing and irrigated cropping land uses at relatively broad-scales (within 5 km, and within 2 km, respectively); lippia's preference for more mesic sites is concordant with its occurrence on clay soils with high moisture-holding capacity in riparian or other locations such as roadside table drains with poor drainage (Earl 2003). While tree size was not included in this study as a predictor term in models, as a response variable it was well-predicted by lippia cover; the converse of this relationship is more probable (i.e. that tree size is a strong predictor of lippia cover). Lippia's relationship with trees in this landscape is investigated more thoroughly in Chapter 6.

5.4.3 Drivers of riparian woodland ecosystem condition

Disturbance

Disturbance gradients within remnants in this landscape are most likely to be associated with flooding, drought or grazing, as described in Chapter 2. There was limited support for flood disturbance as a major driver in this study, which was conducted eight years after the last major flood event and after a series of very dry years. This may not be the case under conditions of normal or above normal rainfall, when there would be a greater expectation of responses such as eucalypt recruitment and potentially higher richness and abundance of a range of drought-sensitive species which may persist in the germinable soil seedbank (Capon and Brock 2006, Capon 2007). Conversely, drought is a more difficult disturbance to define in terms of ecological response, with the possible exception of altered condition responses in long-lived species (e.g. Tyree and Sperry 1988, Horton *et al.* 2001a,b, Rood *et al.* 2000). Poor tree condition was apparent in this study, but showed significant variation across the study area, indicating that some parts of the landscape were better buffered against drought than others. The strong relationship between tree condition and groundwater depth indicates that accessible shallow groundwater is a critical resource for this phreatic species complex, particularly under drought conditions when there is a significant soil moisture deficit. In contrast, loss of species from the extant vegetation may not be indicative of reduced redundancy, except in species which do not form a persistent germinable soil seedbank (Holzel and Otte 2004, Capon 2007) or where the duration of drought exceeds historical norms, when less well adapted species may be selectively filtered from the system (Ooi *et al.* 2009).

Disturbance associated with patch-scale grazing was a strong driver of both tree condition and floristics (alien:native and shortlived:perennial richness transitions, and C4:C3 abundance transitions). Floristic response to grazing in these groups indicate interactions between selective grazing and drought impacts on population processes in short-lived ephemeral species, including alien species, and more mesic C3 species (McIntyre *et al.* 1999b, Fynn and O'Connor 2000). However, different responses in these measures may be evident with normal or above-normal soil moisture conditions, where other studies have reported increased diversity of alien, short-lived and C3 species with medium levels of grazing intensity (e.g. McIntyre *et al.* 2003, McIvor *et al.* 2005). In this study, poor tree condition was predicted by patch-scale grazing (as above) and a greater density of dead trees, confirming the link suggested by Wylie *et al.* (1992) and Davidson *et al.* (2007). However, this is counter to the finding of Fensham (1998b) who found no effect of grazing on the drought mortality of trees in savanna communities in Central Queensland, indicating that the link may be influenced by landscape or environmental context. Higher density of *Acacia stenophylla* seedlings is an unexpected result in grazed remnants, given the findings in Chapter 4, but may be a short-term effect of de-stocking of these remnants due to drought (pers.obs.). Lack of significant response in the forb:tussock grass and clonal:tussock grass functional richness and abundance transitions, previously reported to be sensitive to grazing disturbance (e.g. Ash and McIvor 1998; Clarke and Davison 2004; McIvor *et al.* 2005, Fahrig *et al.* 1994, Rosenthal and Lederbogen 2008), may also be indicative of drought impact.

Land use type and intensity

Surrounding land use/land cover type (e.g. proportion of irrigated cropping and the ratio of cropland to natural vegetation) were strong predictors of tree condition, lippia cover and individual floristic responses. Collard (2007) also reported significant influence on plant species richness and cover associated with agricultural land use pattern surrounding brigalow *Acacia harpophylla* remnants in southern Queensland. In the current study, strong responses to the level of irrigated cropping in the broader landscape were apparent (e.g. higher short-lived:perennial richness and abundance, higher density of *Acacia stenophylla* seedlings); however, both floristic composition and tree condition responded most strongly to the proportion of irrigated and total cropping within 2 km upslope of sites. Upslope land cover and land use may influence the availability of plant propagules for dispersal by rainfall runoff (overland flow). There is likely to be greater richness of disturbance-adapted ephemeral species, as well as higher propagule pressure from these, associated with higher levels of cropping upslope (Cox and Allen 2008). In addition, the influx of materials which promote disturbance-adapted species, including sediments, nutrients and contaminants, is also likely from farming land (e.g. Jones *et al.* 2001). However, this potentially interacts with the presence of overland flow diversions, such as off-stream floodplain water storages and channels associated with irrigated cropping. These have significantly reduced contributions to in-stream flows on the Upper Condamine (Porter 2002), and are strong predictors of richness gradients in short-lived:perennial species and clonal:tussock grass species in this study (below).

Land use intensity in this landscape is largely reflected in high levels of groundwater usage for irrigation purposes, as described in Chapter 2. Numbers of registered groundwater bores within 5 km of sites (GW5000) ranged from 17 to 78, confirming significant pressure on groundwater resources in this landscape (CSIRO 2008). GW5000, as a surrogate for land use intensity, was a strong predictor of poorer tree health (lower average foliage index and higher levels of dieback severity) and of higher relative C4:C3 abundance. Indicators of groundwater demand driven by land use intensity (groundwater depth (GWdepth5000) and groundwater trend (GWtrend5000)), were strong predictors of lower density of mature trees and increased density of dead trees, as well as changes along functional richness and abundance gradients. All three (GW5000, GWtrend5000 and GWdepth5000) were key predictors of overall floristic composition, with mean groundwater depth in 2004-05 explaining 31% of variation in the floristic composition.

Variation in groundwater level is reported to be an important predictor of floristic composition in riparian ecosystems in riparian systems elsewhere. Groundwater levels adjacent to river channels are frequently shallower and more accessible to vegetation than at greater distances from rivers (Wassen *et al.* 2003, Jolly *et al.* 2008), and many riparian species are phreatophytes, either totally dependent or occasionally so on access to groundwater resources. Access to groundwater may be critical for the persistence of these species (Cooper *et al.* 2003b), particularly in seasonally or stochastically variable climates where soil moisture levels may be periodically limiting. Consequently, reduced groundwater access may have significant impacts on community composition in such environments (e.g. Stromberg *et al.* 1996, Elmore *et al.* 2003, 2006a). For example, on the San Pedro River floodplain, an arid zone river in Arizona (USA), groundwater decline due to periodic drought and over-extraction (pumping) from the alluvial aquifer contributed to reduced richness, cover and diversity and altered composition of riparian vegetation (Lite *et al.* 2005, Stromberg *et al.* 1996, 2006). In these studies, the depth, magnitude and rate of groundwater decline are reported to be important parameters; however, in contrast to the current study where groundwater depths ranged from 9 to 19 m, groundwater levels in these studies were relatively shallow (<0.2 m to 7 m), with significant change in species diversity and cover abundance reported with groundwater decline to depths in excess of 0.2 m (Lite *et al.* 2005, Stromberg *et al.* 1996). Significant floristic response to groundwater depth below the average rooting depth of herbaceous groundcover species in riparian woodland remnants on the Upper Condamine, indicates an indirect response potentially mediated through hydraulic redistribution of deeper soil moisture by perennial woody species, as has been reported by Elmore *et al*. (2003, 2006a) and Ludwig *et al.* (2004b). It is suggested that a critical threshold in this system is likely to occur where groundwater depths exceed around 15 m, which previous studies (Mensforth *et al.* 1994, Horner *et al.* 2009) indicate may be the maximum effective rooting depth for *E. camaldulensis*.

Longitudinal and lateral hydrological connectivity

Greater remnant extent in areas upslope of sites was an important predictor of some functional group transitions (i.e. higher C4:C3 richness, but lower clonal:tussock grass, floodplain:terrestrial and wetland:terrestrial richness ratios), potentially indicating greater dispersal of C4, tussock grass, and generalist species from upstream remnants or limitations on the dispersal of C3, clonal, floodplain and wetland species from these remnants. The availability of species propagules upstream may play a critical role in determining the species recruitment patterns and floristic diversity in riparian communities (Xiong *et al.* 2003, Jansson *et al.* 2005, Vosse 2007). This may be especially the case for mesic C3, clonal, floodplain and wetland species which are all likely to be transported predominantly by floodwaters (e.g. Leyer 2006, Stromberg *et al.* 2008). Conversely, species which are not specifically adapted for flood dispersal (e.g. terrestrial species) are likely to be widely dispersed across the landscape by a range of vectors (Drezner *et al.* 2001), or to exhibit no directional pattern where adapted for dispersal by animal vectors whose movements are restricted to riparian habitats (Leyer 2006).

Mesic C3, clonal, floodplain and wetland species are unlikely to have been well-dispersed between riparian communities in the 8-9 years since the last flood event in this landscape in 1996, and functional transitions in these groups may be indicative of a broad shift in the functional diversity of extant vegetation in the absence of major flooding to restore longitudinal and lateral connectivity. However, significant association between the relative richness of these functional groups and the extent of remnant vegetation upslope is indicative of more localized response. Dispersal of species propagules between local plant communities in fragmented landscapes is identified as a critical factor underpinning the function of remnant patches as a metacommunity (Ozinga *et al.* 2004); hence, functional transitions to more generalist species where upslope remnant extent is limited may be indicative of metapopulation failure in more specialized species and ecosystem decline at a larger scale (Wimberly 2006).

An alternative explanation may lie in the greater level of flow diversion due to the presence of water storages, and associated levees and irrigation channels, in cropped areas in the study landscape. Previous studies have shown significant impact on floodplain tree mortality (eg Steinfeld and Kingsford 2008), soil microbial activity (Kang and Stanley 2005) and seedling number and species richness (Leyer 2006) with changes in the lateral extent of overbank flooding due to floodplain infrastructure such as levees, channels and dykes. While not specifically tested in this study, significant localized impacts on riparian community structure and function may also occur where upslope infrastructure impedes overland flood flows and propagule dispersal within the riparian corridor.

Dominant tree condition

Poor tree condition (i.e. dieback severity) was a key predictor of a number of community response variables, including higher relative floodplain:terrestrial richness and abundance, higher relative wetland:terrestrial abundance and lower relative short-lived:perennial abundance, and higher levels of *A. stenophylla* recruitment. The relationship between declining canopy tree condition and floristic composition, particularly the strongly linked transition to a greater abundance of short-lived species relative to perennial species, suggests a similar situation to that reported by Elmore *et al.* (2003, 2006a). In that study, groundwater extraction and declining shallow groundwater levels were associated with decline in perennial herbaceous species, and an increase in short-lived ephemeral species which were significantly more responsive to rainfall (Elmore *et al.* 2003, 2006a); the rate at which this occurred was reduced where deeper-rooted woody vegetation played a facilitative role, accessing shallow groundwater resources and maintaining levels of soil moisture availability through the process of hydraulic lift, thereby buffering the community during drought. In this study, evidence of a similar response to loss of function in dominant deep-rooted woody species supports the role of *Eucalyptus camaldulensis/E. tereticornis* as mediators of soil moisture and floristic response to decline in groundwater at depths well below the average rooting depth of herbaceous groundcover species. The buffering role of these trees is further supported by the relative decline (selective filtering) of ‘terrestrial’ species which are less well adapted to the hydrological extremes of semi-arid floodplains than species which typically occur on floodplains (‘floodplain’ species, as defined in this study) or in floodplain wetlands (‘wetland’ species). These adapted species, which also occur in floodplain grassland and wetland communities independent of the presence of trees, are more likely to be tolerant/resistant to stochastic variations in water availability typical of this landscape. Groundwater decline and poor condition in dominant phreatic species may therefore represent a significant shift in the factors controlling floristic response in these communities, with reduced buffering in periods of drought, greater responsiveness to stochastic rainfall events, and increasing risk of significant change over time.

Lippia abundance

The alien species *P. canescens* (lippia) is a dominant component of floodplain ecosystems of the northern Murray-Darling Basin (Earl 2003, Chapter 2); however, its relationship with floristic composition in native ecosystems has not previously been investigated or reported. In this study, lippia abundance was a key predictor of patterns in overall species composition, explaining up to 17% of variation in the multivariate dataset. Lippia cover was also a strong predictor of functional group transitions, including C4:C3 richness and abundance, short-lived:perennial richness and clonal:tussock grass richness. Dominance by invasive alien species in native vegetation communities is often associated with reduced species diversity (e.g. Clarke *et al.* 2005, Stinson *et al.* 2007, Gooden *et al.* 2009a,b, Hejda *et al.* 2009) driven by direct competition for resources (e.g. Clarke *et al.* 2005, Cordell and Sandquist 2008) or, less frequently, recruitment limitation mechanisms such as allelopathy (Callaway and Ridenour 2004). Hejda *et al.* (2009) assessed the impact of 13 invasive species in the Czech Republic, and found reduced species richness, diversity and evenness in almost all cases and, in some instances, by up to 90%. In Australia, research into vegetation community responses to invasive weed species have found significant changes in floristic composition, species richness and abundance in response to invasion by species such as *Cytisus scoparius* (Wearne and Morgan 2004) and *Lantana camara* (Gooden *et al.* 2009a,b).

In this study, lippia was also a key predictor of larger tree size (mean D_{130}) and reduced density of dead trees; however, these may represent correlations rather than direct cause and effect. Close association between tree size and lippia may be indicative of a facilitative effect on lippia cover by mature trees. Larger trees in this landscape may have greater access to soil moisture, groundwater and nutrients with roots occupying greater soil volumes and extending to greater depths (Meinzer *et al.* 1999). In addition, larger trees are likely to have larger canopies, and potentially act to ameliorate abiotic conditions (e.g. light, temperature, soil moisture, evaporation) beneath their canopies to a greater degree (e.g. Belsky *et al.* 1989, Belsky *et al.* 1993b). These localised effects may facilitate increased cover of lippia, a mesic C3 species (Xu and van Klinken 2008). This is supported by evidence of a negative relationship between lippia cover and dead tree density where these conditions would not be modified to the same extent. The relationship between trees and lippia cover is explored in more detail in Chapter 6.

Functional group transition ratios

Responses in functional group richness and abundance transition ratios were associated with gradients in key environmental disturbance variables, indicating the potential of this approach in facilitating investigations into the dynamics and emergent properties of ecosystems, including redundancy and, potentially, resilience. It enables a space for time approach (e.g. Stromberg *et al.* 1996) which may enable predictions of future ecosystem response to processes already in train, but associated with long lag-times in long-lived dominant species such as canopy dominants, or response to future change associated with predicted shifts in critical climatic conditions. These measures are a novel approach to measuring ecosystem response, based on evidence in the scientific literature of general responses within functional trait groupings to environmental gradients (e.g. Diaz *et al.* 2004). They take contrasting pairs of functional response groups based on species origin (alien, native) and traits, such as life cycle, life form and habitat affinity, to derive ratios of either the richness or cumulative abundance of contrasting functional group pairs (i.e. functional transition ratios), potentially providing a dynamic measure of ecosystem change along (in response to) specific environmental gradients. This study provides evidence of strong association between environmental gradients and a range of functional transition ratios, indicating the potential of this approach to identify change in ecological function or response capacity.

Response to specific environmental gradients is inherent in the organisation of species into functional trait (response, effect) groups (e.g. Pettit *et al.* 1995, McIntyre *et al.* 2003, Rodriguez *et al.* 2003, Bagstad *et al.* 2005, del Pozo *et al.* 2006). Evidence of largely consistent (generalised) patterns in functional group responses to disturbance across a range of ecosystem types (e.g. Diaz *et al.* 2007, Garnier *et al.* 2007) provide a sound basis for further development of this approach. Trait group proportions (of total richness) have been used in similar studies (e.g. McIntyre *et al.* 1995, McIntyre and Lavorel 2001). However, this approach can result in some measures becoming effectively redundant with reciprocals exhibiting inverse environmental relationships, as was noted by McIntyre and Lavorel (2001). This study extends this concept to enable investigation of dynamic responses along functional group transition gradients (i.e. changes in the ratio of richness or total abundance of contrasting functional groups; e.g. C4:C3 species), where endpoints represent maximum (ratio approaches ∞) and minimum (ratio approaches 0) response diversity (effectively, relative redundancy) within a response set (and *vice versa* for its antithesis).

Ratios of contrasting groups, as adopted in this study, integrate dynamic responses in transition group variables (i.e. across a transition spectrum) and may better enable fine scale composition patterns and trends to be investigated in terms of relevant ecological processes. Functional group transition ratios incorporate a fundamental concept of ecosystem resilience (i.e. redundancy) and enable exploration of dynamic functional responses to disturbance and resource availability gradients. Such investigation of community responses to a range of environmental states is effectively a space for time study (e.g. Stromberg *et al.* 1996) which allows predictive insight into the composition and function of current and potential community states in this landscape.

5.4.4 Significance and limitations

Vegetation community studies frequently explore the influence of within-remnant environmental gradients, such as nutrient levels (e.g. Thomson and Leishman 2005) and disturbances associated with fire and grazing (e.g. Wardell-Johnson *et al.* 2004), and have used various modelling approaches to identify key drivers of floristic composition (e.g. Le Brocque and Buckney 1995). However, few (if any) take a broad multivariate approach which incorporates both within-remnant and broader landscape environmental gradients to elucidate ecological change in ecosystems in response to landscape modification (although see Collard *et al.* 2011). This approach may be particularly suited to examining drivers of composition and function in small remnants within a highly contrasting matrix landscape. Riparian woodlands on the Upper Condamine floodplain are highly fragmented, relictual ecosystem remnants (*sensu* McIntyre and Hobbs 1999), subject to significant within-remnant disturbance and surrounded by significant landscape change. The small relative size of these remnants in relation to the surrounding non-remnant agricultural matrix potentially sets them apart from the majority of native ecosystems studied in less highly modified landscapes, and makes consideration of surrounding landscape impacts essential.

The exploratory approach adopted in this study involved choices about which environmental variables were most appropriately included in the model test sets. Selection of potential test variables was based on *a priori* knowledge or established understanding; however, the need to reduce the number of variables to a parsimonious test set, eliminating all but one of any highly correlated variables meant that many variables were ‘discarded’. Choice of variables to retain in test sets in this study was a subjective process, and resulted in large numbers of discarded variables from each of the initial model test sets. Hence, while the results presented are valid, they are not exclusive as additional important relationships may exist with highly correlated variables which were omitted from analysis (e.g. Kuhner and Kleyer 2008, Kath *et al.* 2009).

Groundwater depth appears to play a key role in driving/buffering community responses especially under drought conditions in these communities. In this study, it was the most important driver of overall floristic composition, played a key role in maintaining tree health, and was a key predictor of community structure influencing a range of functional group transitions. The close link between mean groundwater depth, which was in excess of 9 metres, and responses in herbaceous species is likely to be mediated by *E. camaldulensis*, a deep-rooted phreatic tree species capable of hydraulic redistribution (Burgess *et al.* 1998). Groundwater decline beyond the effective rooting-depth of trees may result in the disconnection of canopy trees from this critical water source, resulting not only in greater incidence of dieback (as above), but also secondary impacts on groundcover vegetation reliant on redistributed groundwater particularly during drought. However, additional research is required to identify tree water sources in the Upper Condamine floodplain landscape.

In Australia, altered groundwater levels have been previously reported to impact species richness and diversity only in situations of groundwater rise with associated mobilisation of subsoil salts (e.g. Lymbery *et al.* 2003). Concern regarding the adverse impacts of water resource development on ecosystem health has been associated with reduction in high and medium-level surface water (in-stream) flows, while groundwater research and management has focused on salinisation issues associated with rising water tables due to landscape-level hydrological change. Groundwater decline is generally viewed as a resource management issue impacting water-dependent production systems such as irrigated agriculture. However, detailed understanding of groundwater flows is limited; the links between declining groundwater levels and reduced low level in-stream flows and the associated limitation of surface-groundwater exchange have only recently been explicitly reviewed, and the role of groundwater in supporting water-dependent species and ecosystems appears to be even less well understood. In this study, ‘GWdepth5000’ was a relatively coarse measure (due to a limited number of monitoring bores in the study area) derived by averaging reported 2004-05 groundwater depths across all monitoring bores within 5000 m of survey sites; however, the strength of the relationship between groundwater depth and community response in this study was apparent despite limitations imposed by the poor resolution of groundwater level data. Further research is required to establish depths and conditions under which trees cease to access groundwater and become reliant on surface and subsoil moisture, hence increasingly vulnerable to rainfall variability and physiological failure.

Dominant invasive weed species are often reported to exert significant and detrimental influence on ecosystem composition and function (e.g. Reinhart *et al.* 2006a, Callaway and Ridenour 2004). There has been substantial recent research into the autecology of lippia and its impact in floodplain livestock production systems; however, there has previously been no investigation of the species' impacts within invaded native ecosystems in Australia. This study found lippia cover to be a key driver of floristic composition, explaining up to 17% of variation in the multivariate dataset, and, in combination with other variables, a strong predictor of a number of functional group richness and abundance transitions (C4:C3, short-lived:perennial, clonal:tussock grass). Lippia was also found to have a significant relationship with mature canopy trees in these woodlands, although this was not able to be clearly interpreted in this study. This is explored in more detail in Chapter 6.

Important drivers (i.e. correlates) of ecological responses in tree condition, lippia cover and diversity within floristic functional groups in this study included groundwater depth (and to a lesser extent, the rate of groundwater decline), floodplain development intensity (e.g. the extent of irrigated cropping land uses or the number of registered groundwater bores surrounding survey sites), the proportion of land grazed and the area of mapped remnant vegetation surrounding survey sites. Key relationships identified in this study are summarised in Figure 5.3.

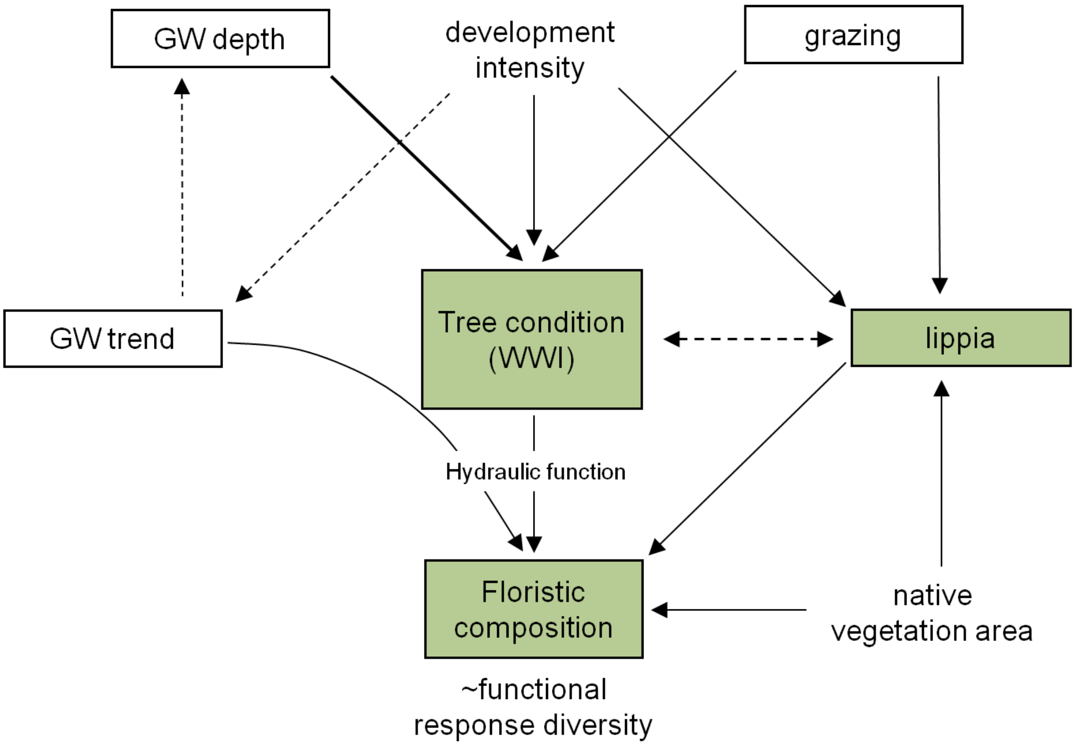


Figure 5.3 Conceptual flow diagram of key environmental factors associated with responses in ecosystem response variables (tree condition as indicated by site Weighted Wylie Index or WWI, lippia cover and floristic composition) in riparian woodland communities on the Upper Condamine floodplain. ‘development intensity’ encompasses GW5000 and irrigcroppn2000; ‘native vegetation area’ encompasses REremppn2000 and grazppn5000 (From Tables 5.6 and 5.10). Vegetation components are shown as shaded. Dotted lines indicate probable relationships not identified in this study; the relationship between lippia and trees is further explored in Chapter 6.

5.5 Conclusions

This study has identified significant association between ecosystem response (composition and condition) variables and a range of environmental variables in remnant floodplain riparian woodlands on the highly modified Upper Condamine Floodplain. Community composition, functional species group richness and abundance and dominant species attributes were generally best-explained by models based on combinations of hydrological and spatial (land use, land cover) variables across a range of local landscape scales, rather than hydrological variables alone, although these were frequently strong predictors within these mixed models.

There was evidence of significant association between ecosystem response (composition and condition) and a number of key environmental variables in these riparian woodland remnants which reflect gradients in levels of resource availability and disturbance, and in the condition and abundance of functionally important dominant canopy (*Eucalyptus camaldulensis/E. tereticornis*) and weed species (*Phyla canescens*). In particular, the impact of groundwater depth and, to some extent, the rate of groundwater decline, was a key predictor in a large number of the ecosystem response models generated, including mature tree health in the dominant canopy species complex *Eucalyptus camaldulensis/E. tereticornis*. This study also identified a link between declining dominant tree condition, groundwater decline and changing patterns in functional diversity. Functional decline due to dieback processes in canopy trees may represent a critical change in these ecosystems with significant implications for the persistence of these dominant species on this section of the floodplain. However, indication that these also mediate response in other species suggests that dysfunction in these ecosystems may be cumulative and potentially self-reinforcing; this is explored further through state and transition modelling in Chapter 7.

This study also indicates the potential for a threshold response, in terms of function in *E. camaldulensis/E. tereticornis*, to groundwater depth; other studies suggest that this might occur at around 12 -15 m for *E. camaldulensis* (Mensforth *et al.* 1994, Horner *et al.* 2009). The significance of such a threshold, in terms of its impact on ecosystem resilience in these communities and the potential for accelerated (cascading) responses in other elements, raises deep concern about the future of these woodlands given the significant pressure on groundwater resources in this landscape (Chapter 2). Further research designed to identify the groundwater depth at which changes in tree condition occur in this landscape, and the environmental conditions under which these are likely to contribute to a threshold response in ecosystem function, is required.

Further complexity is indicated by strong association between *Phyla canescens* (lippia) cover and tree size, and a strong negative relationship between lippia cover and the density of dead trees. While this study was unable to identify strong predictors for lippia cover, apart from surrogate measures which encompassed improved soil moisture conditions, lippia is evidently a strong driver of floristic composition and community structure in these woodlands. In addition, interactions between tree condition and lippia cover may contribute to accelerated change in this landscape; these are further explored in Chapter 6.

Chapter 6 Lippia-tree interactions in an Upper Condamine floodplain riparian woodland

6.1 Introduction

Invasive species represent a significant threat to native ecosystems, contributing to native species decline and altered community composition, structure and ecosystem function (Barney and Whitlow 2008, Whitcraft *et al.* 2008). There are also significant societal costs associated with the control and management of invasive species and their impacts (Pimental *et al.* 2000). However, the drivers of alien species' invasiveness and native ecosystem susceptibility to invasion are often poorly understood (Dietz and Edwards 2006, Strayer *et al.* 2006, Barney and Whitlow 2008). An important factor in invasion success may be interaction between novel species and the receiving environment (e.g. Cavieres *et al.* 2005, Baiser *et al.* 2008). Such interactions may enable invasive species to overcome establishment barriers, and to become naturalised and, in some cases, invasive (Richardson *et al.* 2000, Rudgers *et al.* 2004, 2005). They may also contribute to conditions within an environment which further facilitate the success of the invasive species (e.g. Reinhart *et al.* 2006a).

6.1.1 Species invasion in native ecosystems

The success of alien species in novel ecosystems is, in part, a function of the inherent characteristics (autecology) of the species (i.e. its capacity for invasiveness) (Barney and Whitlow 2008). Invasive plant species frequently exhibit a combination of traits which underpin their success as invaders. These include adaptations for efficient dispersal by wind, water or animal vectors, rapid establishment and growth to reproductive age, the ability to rapidly sequester under-utilised resources, and prolific reproduction (Stohlgren and Schnase 2006).

Time since introduction may also contribute to invader success (Barney and Whitlow 2008). Local increase and establishment of a persistent seedbank provides significant propagule pressure, a key factor in the spread of invasive species (Colautti *et al.* 2006). Some species also modify abiotic conditions in a way that enhances further invasion (MacDougall and Turkington 2005). Both mechanisms have been used to explain observed time lags between initial introduction and establishment in novel environments, and subsequent rapid population growth in invasive species (Reinhart *et al.* 2006a,b, Wangen and Webster 2006).

A third key factor in the success of invasive species is the susceptibility to invasion of native plant communities (Barney and Whitlow 2008). Elton (1958) contended that, in theory, the success of new species would be limited in native environments with high species diversity and niche occupancy. This is evident in some cases (Funk *et al.* 2008) but, in others, invasion success is not significantly affected by species the richness or evenness (e.g. Mattingley *et al.* 2007), or functional diversity (e.g. Dukes 2001), of native environments. Invasion of native habitats is frequently associated with disturbance, which often results in increased availability of resources (Adair *et al.* 2008). Fluctuating levels of resources may be a critical factor influencing the susceptibility of native communities to invasion, particularly when increases coincide with the availability of invasive species propagules (Davis *et al.* 2000, Insauasti and Grimoldi 2006) and match the autecology of the invasive species (Price *et al.* 2010a). Invasive species which become dominant, and alter community structure, ecological processes or abiotic conditions, may contribute to altered resilience and increased risk of significant change in the dynamics and function of invaded ecosystems (Reinhart *et al.* 2006a, b, Rudgers and Orr 2009).

6.1.2 Interactions between native and invasive species

Facilitation is increasingly recognised as an important process which contributes to community diversity and structure, promotes species coexistence and drives community dynamics in native vegetation communities (Callaway 1995, Brooker *et al.* 2008). Such interactions may occur through amelioration of microclimatic conditions, reducing light intensity and evapotranspiration and enhancing the establishment and survival of juvenile plants (e.g. Nunez *et al.* 1999, Phillips and Barnes 2003, Armas and Pugnaire 2005). Alternatively, facilitation may be due to the concentration of resources such as soil nutrients or soil moisture under larger woody species (e.g. Facelli and Brock 2000, Facelli and Temby 2002, Ludwig *et al.* 2003). Vegetation community dynamics driven by the population dynamics of woody perennial species are an important source of spatial heterogeneity in resource limited environments (Facelli and Brock 2000) and may contribute significantly to species coexistence, hence greater diversity, in these systems (Facelli and Temby 2002). This may be especially so in savanna landscapes where scattered trees contribute to significant levels of heterogeneity in terms of resources and micro-climatic conditions (e.g. Facelli and Brock 2000, Graham *et al.* 2004), and may play a major role in facilitating a range of other species (e.g. Ludwig *et al.* 2003, 2004a).

The role of native plant-mediated facilitation in promoting invasion by alien plant species is less well known (Reinhart *et al.* 2006b), but has been shown to be important in some instances. For example, short-lived nitrogen-fixing native bush lupine shrubs (*Lupinus arboreus*) in California coastal prairie communities create nutrient-rich microsites which are readily colonised by annual alien species at the expense of native species as shrubs senesce (Maron and Connors 1996). Invasion success of Scotch broom (*Cytisus scoparius*) in montane shrub communities in New Zealand is facilitated by the presence of native shrubs and tussock grasses (Bellingham and Coomes 2003). Invasion of two *Senecio* species is facilitated in both grassland and shrubland, but not forested, communities in northern Spain in the absence of disturbance (Cano *et al.* 2007).

Such interactions may be more widespread in more stressful environments (Callaway 1995, Scholes and Archer 1997), where native species ameliorate harsh environmental conditions and may contribute significantly to the persistence of invasive species which are not well adapted (e.g. Ludwig *et al.* 2004a, Callaway *et al.* 2003). For example, Badano *et al.* (2007) report facilitation of annual alien species by the cushion plant *Azorella monantha* at higher elevations, in the Andes mountains, Chile. Griffith and Loik (2008) report facilitation of the invasive annual grass *Bromus tectorum* by native shrubs *Artemisia tridentata* and *Purshia tridentata* in the Great Basin Desert, USA. However, these studies also indicate that the relative importance of facilitation (i.e. the balance between facilitation and competitive exclusion of the invasive species), and the strength and direction of native-alien species interactions, may vary with temporal conditions. Ludwig *et al.* (2004a) report a fine balance between competitive and facilitative interactions in savanna landscapes in East Africa, where competition for scarce water between neighbouring species was shown to overwhelm the facilitative effect of hydraulic lift. Griffith and Loik (2008) also found that both positive and negative interactions occurred, over a period of several years, between *Bromus tectorum* and native shrubs in the Great Basin Desert, USA.

6.1.3 Lippia on the Upper Condamine Floodplain

Many introduced (alien) plant species have been recorded in the Upper Condamine (Phillips and Moller 1995, Fensham 1998a). However, of particular concern in riparian areas of the floodplain is the dominant invasive species lippia (*Phyla canescens* (Kunth) Greene: Verbenaceae) (McCosker 1996), a low-growing perennial clonal herb, native to floodplain environments of South America (Macdonald 2008). First recorded at Tummaville (within the Upper river section of this study) in 1927 (Lucy *et al.* 1995, Earl 2003), lippia was increasingly viewed as a significant problem from the 1950s onward, infesting an estimated 40,000 ha in 1960 and 150,000 ha by the mid-1990s, at which time it was considered a serious and largely unmanageable risk to both pastoral enterprises and to riverine and riparian ecosystems on the Upper Condamine Floodplain (Lucy *et al.* 1995). In invaded floodplain communities (wetlands, grasslands, riparian woodlands) and landscapes of the Murray-Darling Basin, it significantly compromises remnant ecosystem condition, streambank stability and riverine water quality, pasture productivity and the profitability of grazing enterprises, as well as the integrity of floodplain infrastructure (roads, dams, levees) (Earl 2003).

Considerable research has been conducted into the autecology of lippia since the establishment, in 2002, of the National Lippia Working Group, a consortium of land managers and researchers. This has included investigations into the species' reproductive ecology (Macdonald 2008, Gross *et al.* 2010), responses to top-down (enemies) and bottom-up (nutrient availability) control (Clech-Goods 2010), population genetics (Fatemi *et al.* 2008) and adaptive capacity (Xu *et al.* 2010a) in the species' invaded range, and investigation of potential bio-control agents in the species' native range (Julien *et al.* 2004). Lippia's capacity to inhibit the germination of other species through the production of allelopathic chemicals has also been tested (Tan *et al.* 2007). Investigations into lippia's response to disturbance regimes (e.g. flooding and grazing) have been conducted under controlled experimental conditions (Taylor and Ganf 2005) and within working (floodplain grazing) production systems (Price *et al.* 2008, 2010a). These studies also investigated the relative success of lippia and other dominant species under different levels of disturbance (Taylor and Ganf 2005, Price *et al.* 2008).

Lippia in Australia is a genetically diverse species (Fatemi *et al.* 2008) which is rapidly adapting to the variable climatic (and eco-hydrological) conditions across its invaded distribution (Xu *et al.* 2010a). It responds positively to disturbances such as flooding and grazing (Taylor and Ganf 2005, Barry *et al.* 2008, Macdonald 2008, Price *et al.* 2008, 2010a), but is sensitive to competition from other dominant species under certain conditions (Taylor and Ganf 2005, Price *et al.* 2010a). Modeling in relation to predicted climate change indicates that lippia poses an ongoing threat to native vegetation and production systems throughout the Murray-Darling Basin due to a persistent propagule bank and the species' capacity for population explosions following flood events of suitable duration and depth (Stokes *et al.* 2007, 2008, Barry *et al.* 2008, Macdonald 2008). Nutrient availability (specifically nitrogen) enhances lippia's success (Clech-Goods 2010), and clonal integration supports continued growth of ramets exposed to resource-poor (low light) conditions (Xu *et al.* 2010b). Lippia may alter soil attributes, such as soil moisture and carbon isotope signature, under field conditions (Xu and Van Klinken 2008). It also produces secondary compounds with allelopathic properties which affect the germination of some indicator species (e.g. leguminous species such as vetch and subterranean clover) but not others (e.g. grass species such as sorghum) under controlled experimental conditions (Daley *et al.* 2005, Tan *et al.* 2007), although it remains unclear from these trials to what extent these mechanisms contribute to the species' invasion success.

Most lippia research has been driven by the species' significant impact on the productivity of floodplain grazing production systems (Lucy *et al.* 1995, Earl 2003). Research has focused on interactions between flooding and grazing, which have been found to be major factors in the dispersal, establishment and local expansion of lippia (e.g. Macdonald 2008, Price *et al.* 2008, 2011). There has been limited research in native vegetation systems aimed at understanding what impact lippia has on the composition, structure and ecological function of invaded ecosystems. In addition, no research to date has sought to identify the role played by these ecosystems in facilitating the persistence of lippia, particularly in parts of the landscape which are not subject to regular grazing or flooding.

6.1.4 This research

Earlier chapters have shown lippia to be a dominant component of remnant riparian woodland ecosystems on the Upper Condamine floodplain, where it has a significant homogenizing effect on floristic diversity (Chapter 3) and is a key predictor and potential driver of change in floristic composition and structure (Chapter 5). Lippia cover was also found to be highly correlated with mature tree size (Chapter 5), highlighting a potential interaction between trees and lippia and calling into question the role of mature trees in facilitating lippia persistence and abundance in this landscape. This is supported by observations that lippia, a mesic C3 species (Earl 2003, Xu and van Klinken 2008), persists in riparian remnants of the Upper Condamine, often as a ‘halo’ (*sensu* Majer and Delabie 1999) of high lippia cover under the canopy of scattered trees in this landscape, despite grazing exclusion and extended drought (pers. obs.). The question arises, therefore, as to what role, if any, trees may play in the success of lippia in the climatically variable dryland riverine/riparian environments of the Upper Condamine, and potentially elsewhere in the northern Murray-Darling Basin.

Observations that lippia is often also more persistent in lower lying parts of the study area indicate that microtopographic variations in the land surface may also act as spatial and temporal refugia for lippia relative to areas higher in the landscape which experience more variable soil moisture conditions. Elsewhere, small-scale topographic heterogeneity buffers the impact of adverse conditions on vegetation and contributes to native species persistence in salinity-affected landscapes (Cramer *et al.* 2004), and enhances survival and growth of eucalypt seedlings in a microtopographically variable gilgaied floodplain landscape after flooding and fire (Fox *et al.* 2004).

This study asks if there is a positive interaction between dominant canopy eucalypts (*E. camaldulensis/tereticornis*), and the cover of lippia (*Phyla canescens*) in riparian woodlands on the Upper Condamine floodplain, and, if so, does this influence change with topographic position in the landscape or the presence of non-lippia vegetation? It also asks which environmental variables influenced by the presence of trees and/or position on slope are associated with high lippia cover and reproduction, and whether this influence varies with tree size or condition.

The specific hypotheses addressed are:

(i) that lippia (abundance, reproduction, growth form and/or condition) and community (groundcover richness, abundance and diversity) response and environmental variables (soil attributes, nutrients, soil moisture, light) vary along a gradient of increasing distance from trees and/or with topographic position; and

(ii) that there is a correlation between tree size and/or tree condition, environmental variables and biotic responses, including lippia abundance and reproduction.

Results are interpreted in relation to lippia’s adaptive response to fluctuating climatic conditions and levels of disturbance, and the dynamics of lippia-invaded woodlands in this landscape. Potential risks to downstream environments, associated with persistent lippia populations in headwater catchments, are considered.

6.2 Methods

6.2.1 Study area

This study was conducted at St Ruth Reserve, a state-owned reserve (R81) adjacent to the Condamine River and approximately 10 km south of Dalby, southern Queensland (Figure 6.1).

Figure 6.1 Aerial photograph indicating the general location of transects (●) at St. Ruth Reserve.

St. Ruth Reserve comprises a 150 ha patch of remnant riparian and floodplain grassy woodland (predominantly RE 11.3.25; Sattler and Williams 1999), originally used for watering and resting traveling stock (Moran 1996) and, more recently, leased on a semi-permanent basis for livestock (cattle) grazing (Queensland Murray-Darling Committee (QMDC) 2005). Persistent over-stocking and over-grazing on the reserve resulted in significant change in groundcover composition and structure, from tall native perennial tussock grasses to a low-growing lippia-dominant ‘carpet’ (Moran

1996, QMDC 2005). Increasing concern about the proliferation of lippia, in combination with evidence of significant tree decline, led to revoking of the grazing lease and reclassification of the site as a state recreation reserve in 1999 (QMDC 2005). Woodland condition on the reserve has shown signs of recovery following grazing exclusion (QMDC 2005). There is evidence of recruitment of canopy eucalypt species, although recovery of mature *E. camaldulensis/tereticornis* trees is limited and, in many cases, dieback symptoms have continued to increase over the period of this research (2004–2007) (pers. obs.). There has also been a significant decline in lippia abundance post grazing exclusion (QMDC 2005) and a reciprocal increase in the relative abundance of other species, including native perennial grasses (pers. obs.). This has coincided with prolonged drought, which may have contributed to lippia decline. High lippia cover is only evident (persists) in lower lying areas or in association with trees (pers. obs.).

6.2.2 Lippia-tree relations

Study design

This study used a 2-factor design to test for significant patterns in vegetation composition, including lippia cover and condition, and abiotic conditions in relation to trees (‘distance from tree’ treatments) and relative elevation (topographic position treatments). Twelve transects, each extending from the base of a mature tree (*E. camaldulensis/E. tereticornis*), were established within a homogeneous patch of open woodland; distance from tree treatment levels were defined as multiples of the canopy radius (r): 0r, 0.5r, 1r, 1.5r, 2r and 3r (Figure 6.2). Four transects were located in each of three relative topographic positions: Low, Mid (intermediate) and High (with a maximum topographic variation across these of less than 3 m). The length of each transect was determined by the canopy radius (‘r’ or the distance from tree base to canopy edge) along the transect line for that tree, and extended from the tree base into open grassland to a total distance of 3r (maximum r was 8 m and maximum transect length was 24 m). Transect direction was restricted to a south-westerly direction to reduce variation due to possible shading and slope. Tree selection was constrained by proximity of the transect to other trees; only transects which could be established at distances of greater than three times the canopy radius of adjacent trees were included in the study (Figure 6.2).

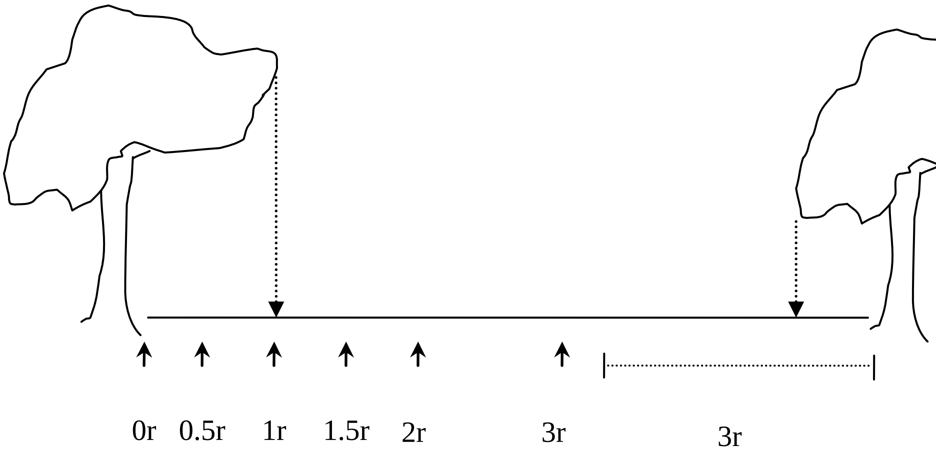


Figure 6.2 Transect design indicating distance from tree treatments based on multiples of r, the canopy radius, and limits in terms of proximity to neighbouring trees.

There were no significant differences in tree height, tree diameter, canopy radius or canopy cover between topographic positions (ANOVA, $p > 0.05$; Table 6.1).

Table 6.1 Attributes of transect trees across topographic position treatments. Treatment values are means and standard error (in parentheses). Significant difference is indicated in bold type (ANOVA; ** $p \leq 0.005$, * $p \leq 0.05$).

	Units	**Topographic position**			**Levene's**	**F**
		low	**mid**	**high**		
Tree height	m	20.0 (1.8)	23.3 (2.3)	24.6 (3.6)	1.75^{ns}	0.78^{ns}
Tree diameter (D130)	m	0.70 (0.18)	0.95 (0.06)	0.83 (0.19)	0.95^{ns}	0.67^{ns}
Canopy radius	m	4.5 (0.3)	3.8 (0.6)	5.0 (1.1)	1.37^{ns}	0.72^{ns}
Canopy cover (FPC)[1]	%	33.0 (2.2)	14.5 (4.8)	23.0 (7.5)	2.21^{ns}	3.03^{ns}

[1] arcsin transformed

Data collection

Sampling was conducted in March 2006. Projected foliage cover (FPC%) of all non-woody vascular plant species was recorded in 1 m^2 quadrats at the six 'distance from tree' treatments (0r, 0.5r, 1r, 1.5r, 2r and 3r) along each transect. Plant species were identified, and grouped according to origin (native, alien) and functional response traits (physiology, life-cycle, growth form) as reported in Chapter 3. Species richness, abundance (cover) and Shannon-Wiener diversity were calculated as reported in Chapter 3.

Lippia condition and reproductive effort were recorded in 0.25 m^2 quadrats centred within the 1 m^2 quadrats used above. Measures included the number of flower heads and seed heads (the total of which is referred to as 'reproductive effect'); evidence of herbivory, disease and discolouration (yellowing), scored on a 4-point scale (0: none, to 3: severe; after Batterham 2008); and dominant growth habit ('matting' or 'trailing'; equivalent to the 'phalanx' and 'guerrilla' growth forms of Chen *et al.* (2010), and the 'established' (rooted) and 'infiltrated' (supported above the soil by neighbouring vegetation) forms of Taylor and Ganf (2005)).

The circumference, height, canopy radius (along the transect line, to the nearest 0.5m) and canopy projected foliage cover (FPC%) of each transect tree was measured. Ambient light (measured beyond tree canopies and above the height of groundcover vegetation) and incident light at ground level were measured at two sampling points along each transect, nominally 0.5r (but measured in the centre of the canopy shade at the time of measurement) and 2r, using a line quantum sensor (Li-191, Li-Cor 2005). This equipment averages incident light over its 1 m length and is suited to measurement in dappled shade conditions as occur under relatively sparse canopies (LiCor 2005). The ratio of incident light at ground level to ambient light above the vegetation was used to account for temporal variation in light intensity.

Soil moisture was measured at three depths at each transect sampling point. Surface (0-6 cm depth) sample measurements were taken using a soil moisture impedance probe (Theta Probe; Delta-T Devices, Cambridge, UK). Deeper soil moisture measures were taken using electromagnetic induction (EMI) equipment (EM38; Geonics Ltd, Canada), which measures the apparent bulk electrical conductivity (ECa) of the soil profile, providing an integrated measure of soil salinity, clay content and soil moisture through the soil profile (Ganjegunte and Braun 2010). As EMI is sensitive to variation in soil moisture, the technique has been used to investigate differences in soil moisture within a defined area (Reedy and Scanlon 2003, Huth and Poulton 2007); this is considered a valid technique for use under non-saline conditions where responses are independent of conductivity (McNeill 1980, Huth and Poulton 2007). The EM38 has a horizontal and a vertical dipole, measuring EC_a to depths of 75 cm and 150 cm, respectively (Reedy and Scanlon 2003, Ganjegunte and Braun 2010). No temperature corrections were made to readings (Reedy and Scanlon 2003, Huth and Poulton 2007) as this study was concerned only with relative rather than absolute inferred soil moisture.

Surface soil samples were collected for analysis of physical and chemical composition. Samples were collected within a 1 m^2 area at two ‘distance from tree’ sampling points (0.5r and 2r) per transect. Shallow samples (to 15cm) were collected using a foot corer, and deeper samples (at 30-70cm) were collected using a ute-mounted 37 mm diameter hydraulic soil corer. Deep soil samples were collected from four transects only (two from Low and two from High topographic positions) due to cost and equipment availability constraints. Individual samples were placed in labelled sealed plastic bags, and kept cool in an esky to minimise loss of moisture and nitrogen. Analysis of a range of chemical and physical properties (Table 6.2) was conducted by AgriTech, Toowoomba Qld.

Table 6.2 Soil attributes measured in shallow soil and subsoil samples collected from St Ruth Reserve.

Parameter	Units	Shallow samples	Deep samples
Texture	-	✓	✓
pH	-	✓	✓
Electrical Conductivity	dS/m	✓	✓
Magnesium	mg/kg	✓	
Exchangeable Calcium	meq/100g	✓	
Exchangeable Sodium	meq/100g	✓	
Exchangeable Potassium	meq/100g	✓	
Exchangeable Magnesium	meq/100g	✓	
Sulphur	mg/kg	✓	
Nitrate Nitrogen	mg/kg	✓	✓
Chloride	mg/kg	✓	
Phosphorus	mg/kg	✓	✓
Calcium	mg/kg	✓	
Sodium	mg/kg	✓	
Potassium	mg/kg	✓	
Cation Exchange	meq/100m	✓	
Organic Carbon	%	✓	✓

Data analysis

Patterns in floristic composition were investigated using multivariate analysis procedures in PRIMER, version 5 (Clarke and Warwick 2001). Ordination was conducted by non-metric multi-dimensional scaling (nMDS), with similarity matrices constructed (data standardised, no transformations) using the Bray-Curtis similarity measure. Floristic patterns associated with distance from tree and topographic position treatments were investigated using Analysis of Similarity (ANOSIM and 2-way crossed ANOSIM). SIMPER was used to examine lippia's influence on species composition.

Differences in univariate measures of lippia cover, lippia reproductive effort, species richness, total cover, non-lippia cover and Shannon-Wiener diversity were compared across treatments using 2-way Analysis of Variance (2-way ANOVA) procedures in SPSS version 18.0 for Windows (SPSS Inc. 2009). Bounded (proportional) data were arcsine transformed, and all data were screened and transformed (either square root or $\log_{10}$), where required, to meet assumptions of normality and homoscedascity (Quinn and Keogh 2002). Where heteroscedastic variances were unable to be corrected for by transformation, no further analysis was undertaken (Quinn and Keogh 2002). Where variances were homogeneous (Levene's), 2-way ANOVA was conducted and Tukey's unplanned multiple comparison procedure (Day and Quinn 1989) was used to determine significant difference between treatment pairs within distance from tree and topographic position treatments.

The non-parametric Kruskall-Wallis procedure for *k*-independent samples was used to test for significant association between distance from tree or topographic position treatments and lippia condition scores (Quinn and Keogh 2002); the non-parametric Mann-Whitney U procedure was used to determine significant difference between treatment pairs where significant difference was evident (Day and Quinn 1989).

Differences in univariate abiotic (soil chemistry, moisture, light) attributes (transformed where necessary, as above) between sampling positions (0.5r, 2r) and topographic positions (low, mid, high) were investigated using 2-way ANOVA with Tukey's unplanned multiple comparison procedure where appropriate (as above).

Significant association between lippia cover, reproductive effort, tree size and condition and measured environmental (abiotic, biotic) variables was investigated using the non-parametric Spearman's rank correlation procedure in SPSS version 18.0 for Windows (SPSS Inc. 2009).

6.3 Results

6.3.1 Floristic patterns

A total of 44 plant taxa, comprising 35 native and 10 alien species, was recorded in this study (Appendix E). The most frequent and abundant species/taxon recorded was lippia (*Phyla canescens*), with a total frequency of 96% (present in 69 of 72 quadrats) and an overall mean abundance of 27.9 ± 3.4% (range: 0 – 97%). The next most common alien species was *Glandularia aristigera* (Mayne's pest; Verbenaceae) with a frequency of 31% and mean abundance of 2.2% ± 0.8%. The most common native species were *Paspalidium distans* (frequency: 71%; mean abundance: 11.4 ± 2.3%), *Einadia* spp. (frequency: 68%; mean abundance: 8.2 ± 1.7%), and *Cynodon dactylon* (frequency: 65%; mean abundance: 5.5 ± 1.3%).

Floristic composition

There was no significant interaction effect between distance from tree and topographic position treatments on multivariate floristic composition (FPC) (2-way crossed ANOSIM; $p > 0.05$). There were significant differences in floristic composition between distance from tree treatments (ANOSIM; Global $R = 0.194$, $p = 0.001$); there were significant differences between 0r and 0.5r, 1r, 1.5r, 2r and 3r, and between 0.5r and 1.5r, 2r, and 3r, but no differences between 1r, 1.5r, 2r, and 3r distances (pairwise tests, $p \leq 0.05$, Table 6.3). There were no differences between topographic position treatments (ANOSIM; $p > 0.05$).

Table 6.3 Results of Analysis of Similarity (ANOSIM) pairwise comparisons on FPC data for distance from tree treatments. Values are R statistics, with significance levels indicated (** $p \leq 0.005$, * $p \leq 0.05$, n.s. = $p > 0.05$).

Distance from tree	0r	0.5r	1r	1.5r	2r
0.5r	**0.21****				
1r	**0.44****	0.05 ^{ns}			
1.5r	**0.58****	**0.19****	-0.04 ^{ns}		
2r	**0.54****	**0.17***	-0.03 ^{ns}	-0.09 ^{ns}	
3r	**0.60****	**0.24****	0.05 ^{ns}	-0.01 ^{ns}	-0.07 ^{ns}

An nMDS ordination of floristic composition by distance from tree treatments indicates clustering of sites at distances of 0r and 0.5r, and greater spread in the 1r, 1.5r, 2r and 3r treatments (Figure 6.3).

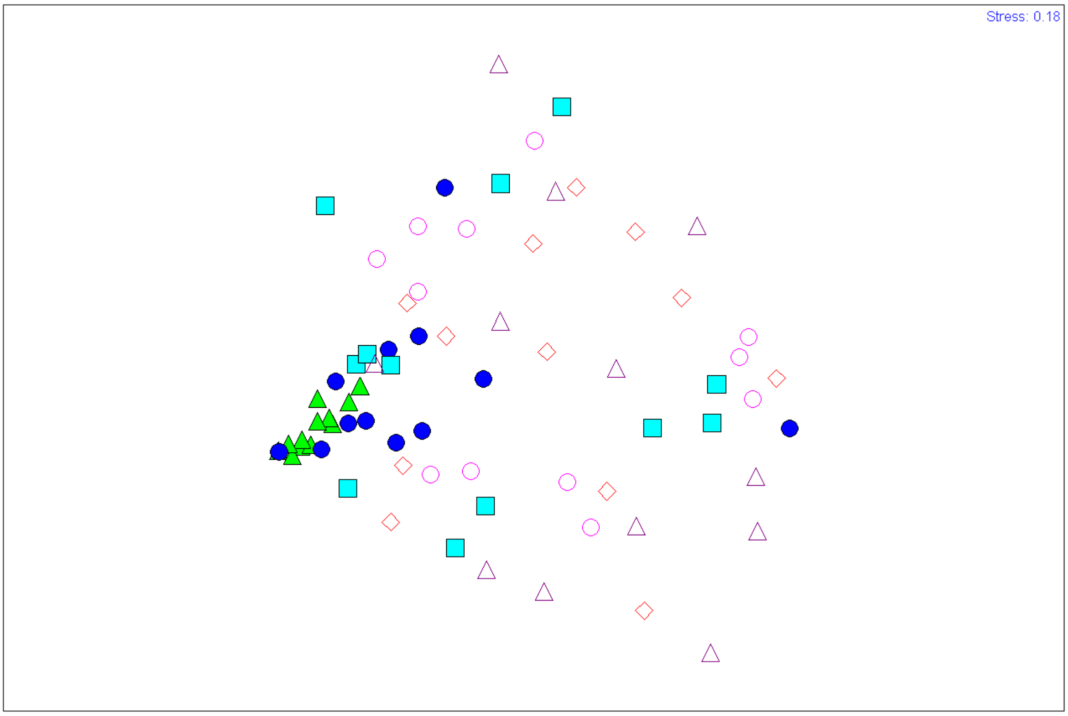


Figure 6.3 Two-dimensional ordination (nMDS) of floristic abundance (FPC) x distance from tree. Filled symbols are 'under canopy' distance from tree treatments: 0r (▲), 0.5r (●), 1r (■); open symbols are 'canopy gap' distance from tree treatments: 1.5r (△), 2r (○), 3r (◇).

The average similarity of floristic composition was greatest (exceeding 50%) within the 0r and 0.5r distance from tree treatments, and least (< 40%) within the 1r, 1.5r, 2r and 3r treatments (SIMPER, Figure 6.4). Lippia cover contributed strongly to similarity (lippia contribution > 80%) within the 0r and 0.5r treatments, but least (lippia contribution < 50%) within the 1r, 1.5r, 2r and 3r treatments (Figure 6.4).

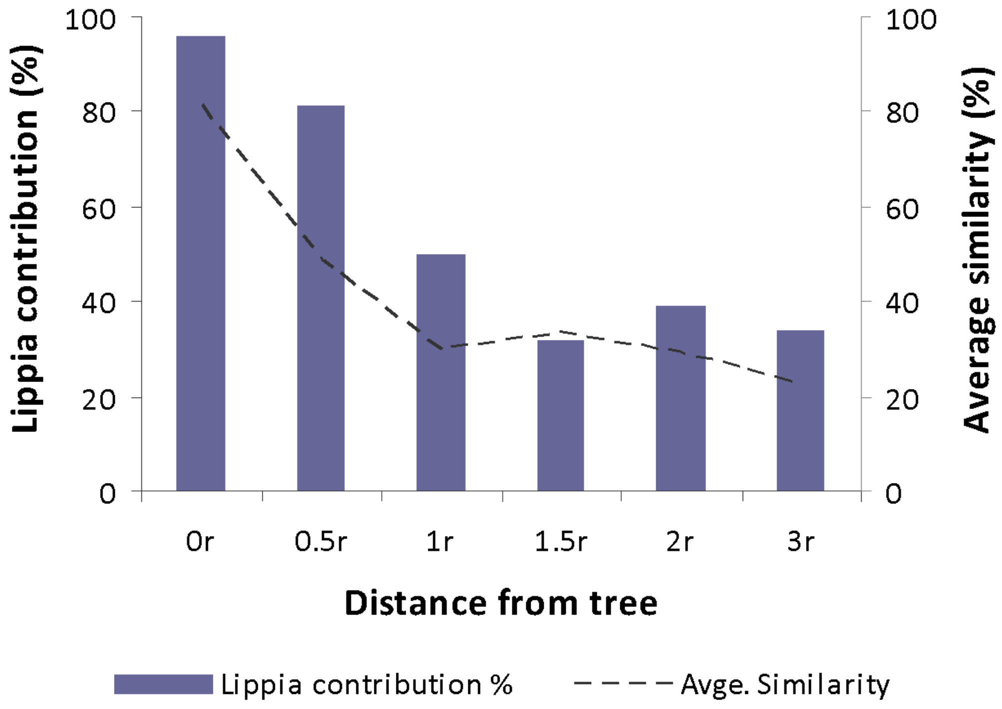


Figure 6.4 Average floristic similarity and lippia contributions to average similarity (SIMPER analysis in PRIMER) within distance from tree treatments.

Differences between distance from tree and topographic position treatments for lippia cover and total Shannon-Wiener diversity were not able to be statistically tested due to non-homogeneous variances (Levene's, $p \leq 0.05$) which could not be corrected by data transformation (Table 6.4). Mean lippia cover was higher (21.8% to 72.3%) but more variable at distances closer to trees (standard error was between 6.6% and 7.9% for the distances 0r, 0.5r and 1r) than at distances 1.5r, 2r and 3r, where cover and standard error values were lower (8.3% to 15.8% and 2.3% to 4.8%, respectively) (Table 6.4).

There were no significant interactions between distance from tree treatments and topographic position for total cover, non-lippia cover, non-lippia species richness or non-lippia Shannon-Wiener diversity (2-way ANOVA, $p > 0.05$; Table 6.4).

There was no significant difference between distance treatments for total cover (2-way ANOVA, $p > 0.05$; Table 6.4). The cover of non-lippia vegetation was significantly lower beneath tree canopies (at 0r and 0.5r) and higher at the tree canopy edge and beyond (1r – 3r), although there was no significant differences between non-lippia cover at 0.5r and 2r ($p > 0.05$). There was no significant difference between topographic positions in the cover of non-lippia species ($p > 0.05$). There was no significant difference in non-lippia species richness or non-lippia Shannon-Wiener diversity between distance from tree or topographic position treatments ($p > 0.05$, Table 6.4).

Table 6.4 Differences between distance from tree and topographic position treatments for lippia cover; total species richness, cover and Shannon-Wiener diversity; and non-lippia species richness, cover and Shannon-Wiener diversity. Treatment values are means and standard error (in parentheses); interaction values are F values. Significant difference is indicated in bold type (** $p \leq 0.005$, * $p \leq 0.05$).

	Distance from tree (D)						**Topographic position (T)**			**Interaction**
	0r	**0.5r**	**1r**	**1.5r**	**2r**	**3r**	**low**	**mid**	**high**	**D*T**
Lippia cover[1,4]	72.3 (6.7)	38.8 (7.9)	21.8 (6.6)	15.8 (4.8)	10.8 (2.3)	8.3 (2.6)	24.5 (4.2)	29.1 (6.9)	30.2 (6.6)	
Species richness	6.4 (0.8)	7.9 (0.8)	8.7 (1.0)	9.8 (0.9)	9.2 (0.8)	9.1 (0.7)	9.0 (0.5)	8.8 (0.7)	7.7 (0.6)	0.09 ^{ns}
Total cover	86.8 (7.7)	63.1 (8.7)	74.3 (8.8)	76.7 (7.6)	56.9 (5.9)	63.0 (8.1)	66.4 (6.1)	75.1 (6.4)	68.9 (4.7)	0.43 ^{ns}
Shannon-Wiener diversity[4]	0.6 (0.1)	1.1 (0.2)	1.2 (0.1)	1.4 (0.1)	1.5 (0.1)	1.4 (0.1)	1.3 (0.1)	1.3 (0.1)	1.0 (0.1)	
Non-lippia richness	5.4 (0.8)	7.0 (0.8)	7.7 (1.0)	8.8 (0.9)	8.2 (0.8)	8.3 (0.6)	6.7 (0..6)	8.0 (0.5)	7.9 (0.7)	0.10 ^{ns}
Non-lippia cover	**14.6^{a} (2.7)**	**24.3^{ab} (5.4)**	**52.5^{c} (9.5)**	**60.8^{c} (9.1)**	**46.2^{bc} (6.7)**	**54.8^{c} (8.4)**	41.9 (6.3)	46.0 (6.7)	38.7 (5.4)	0.74 ^{ns}
Non-lippia diversity	1.0 (0.2)	1.3 (0.2)	1.1 (0.2)	1.3 (0.1)	1.3 (0.1)	1.3 (0.1)	1.0 (0.1)	1.2 (0.1)	1.4 (0.1)	0.30 ^{ns}

[1] arcsin transformed; [2] square root transformed; [3] log10 transformed; [4] hereroscedastic variance (Levene's, $p \leq 0.05$) not able to be corrected by transformation

Lippia reproduction and condition

Mean lippia reproductive effort was not able to be statistically tested due to non-homogeneous variances (Levene's, $p \leq 0.05$), which were unable to be corrected by data transformation. Reproductive effort was high but variable at the under-canopy (0r and 0.5r distance from tree) positions, and consistently low at distances beyond the tree canopy (1.5r, 2r and 3r) (Figure 6.5). There was also a highly variable topographic effect with 39.8 ± 10.2 flower and seed heads at Low topographic positions, 46.8 ± 12.2 at Mid positions, and 57.2 ± 17.4 at High positions. No lippia seedlings were observed.

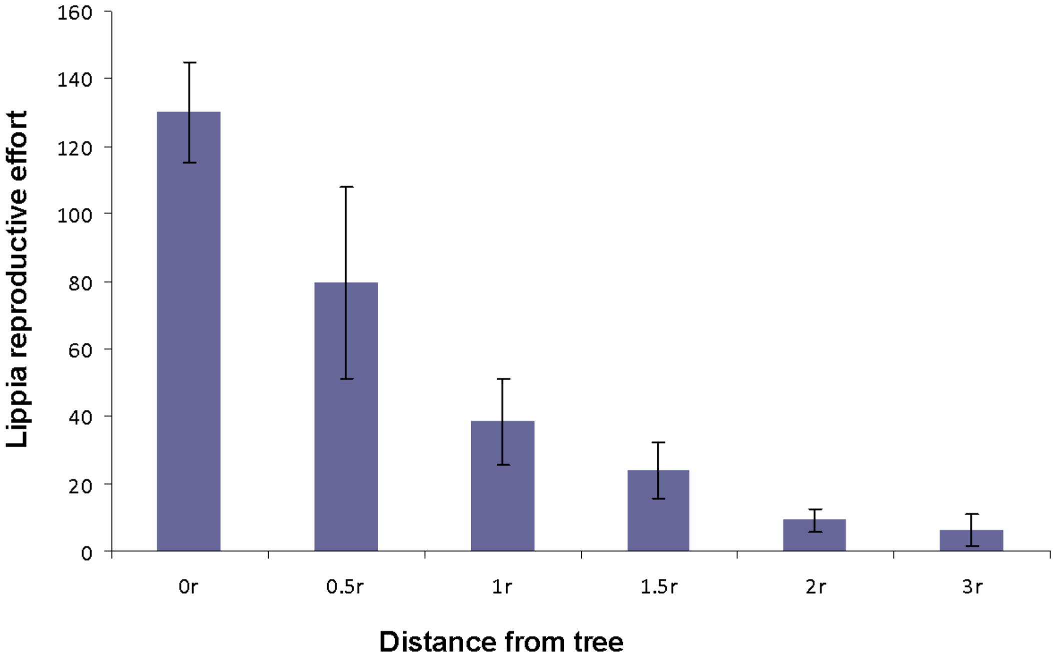


Figure 6.5 Lippia reproductive effort (number of flower and seed heads) with distance from tree treatments. Errors are standard error.

Lippia growth habit scores were significantly lower at distances closest to trees (0r, 0.5r), and higher at the canopy edge and beyond (1r to 3r) (Kruskal-Wallis; $p \leq 0.005$, Table 6.5). No evidence of disease was observed, and there were no significant differences between distance from tree treatments for lippia herbivory or leaf colour scores ($p > 0.05$). There were no significant differences between topographic positions for any of these measures ($p > 0.05$, Table 6.5). Graphical exploration (Quinn and Keogh 2002) indicated no interaction between treatment factors.

Table 6.5 Mean lippia condition response (scores: 0-4) to distance from tree and topographic position treatments. Values are means with standard errors in parentheses; values bearing the same superscript are not significantly different (Kruskal-Wallis, $p > 0.05$)

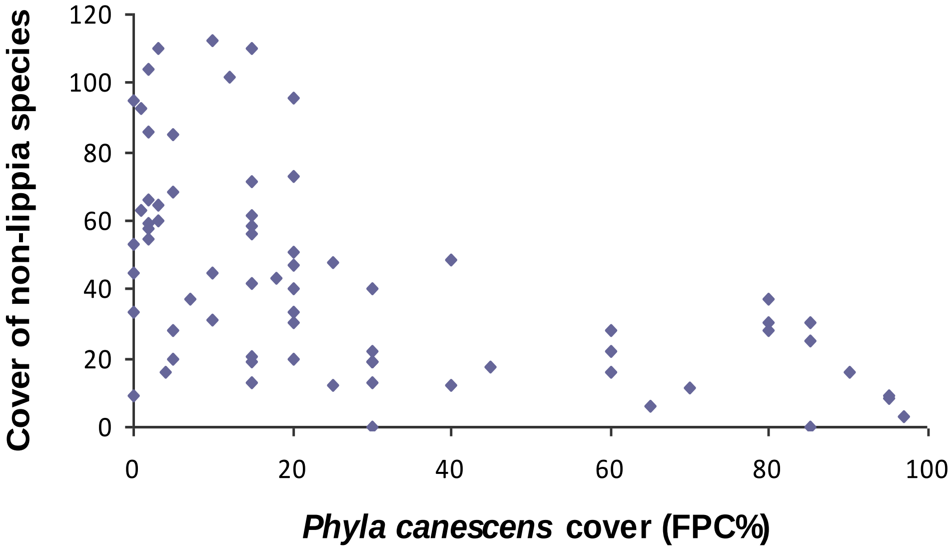
	Distance from tree						**Topographic position**		
	0r	**0.5r**	**1r**	**1.5r**	**2r**	**3r**	**low**	**mid**	**high**
Herbivory	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.1 (0.1)	0.3 (0.1)	0.2 (0.1)	0.0 (0.0)	0.2 (0.1)	0.2 (0.1)
Disease	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Foliage colour	0.3 (0.1)	0.9 (0.1)	0.8 (0.2)	0.8 (0.1)	0.9 (0.2)	0.8 (0.2)	0.9 (0.1)	0.8 (0.1)	0.6 (0.1)
Habit[1]	**1.8^{a} (0.1)**	**2.3^{b} (0.1)**	**2.9^{c} (0.1)**	**2.9^{c} (0.1)**	**3.3^{c} (0.1)**	**3.3^{c} (0.1)**	2.9 (0.1)	2.6 (0.1)	2.8 (0.2)

[1] Low habit score indicates predominantly matting growth form; high habit score indicates predominantly trailing exploratory growth form.

Correlation between floristic response variables

Lippia cover (FPC%) and lippia reproductive effort were significantly correlated (Spearman's; rho = 0.77, $p \leq 0.005$). Lippia cover was significantly negatively correlated with non-lippia cover (total cumulative cover less lippia cover) and Shannon-Wiener diversity (rho = -0.62 and -0.44, respectively; $p \leq 0.005$; Figure 6.6). There was no significant correlation between lippia cover and non-lippia species richness (rho = -0.19, $p > 0.05$).

(a)



(b)

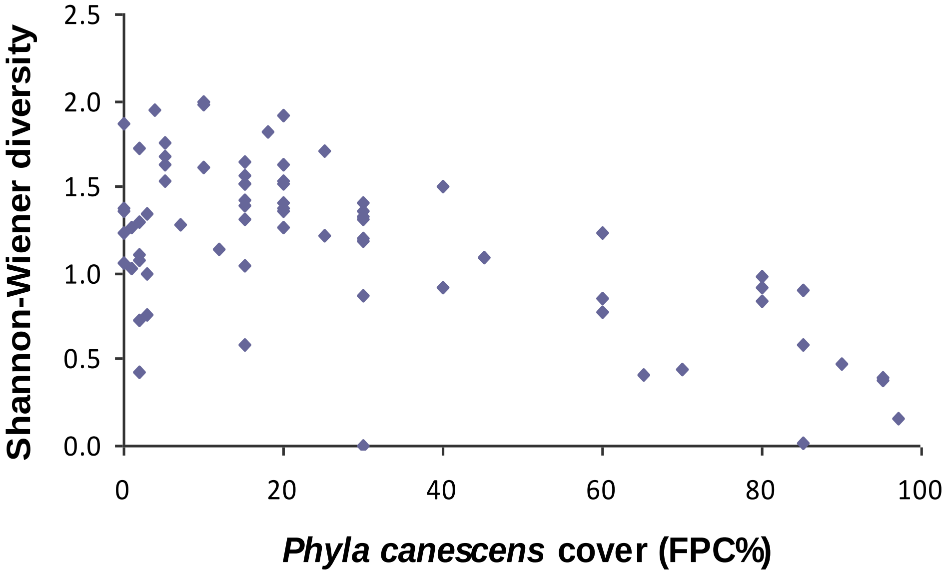


Figure 6.6 Scatter plots showing linear correlation between lippia *Phyla canescens* cover (FPC%) and (a) cover of non-lippia species (FPC%) (r^2 = 0.30), and (b) Shannon-Wiener diversity (r^2 = 0.39).

Lippia cover (FPC%) was negatively correlated with the cumulative cover and species richness of the majority of functional and origin groups tested, including non-lippia alien species (Table 6.6). These correlations were strongly significant for richness of C4 species and cover of native species, perennials, C3 species, graminoids, and short-lived (annual, biannual) species (Spearman's, $p \leq 0.005$), and moderately significant for richness of native and short-lived (annual, biannual) species and cover of clonal species ($p \leq 0.05$). Significant correlations between non-lippia groups were all positive (Table 6.5).

Table 6.6 Spearman's correlations between lippia cover and non-lippia functional and origin species groups richness and cover (FPC%). Values are rho; significant correlations are indicated in bold type (** $p \leq 0.005$; * $p \leq 0.05$).

	Lippia	Alien	C3	C4	clonal	forb	gram.	legume	native
Richness									
Alien	-0.08								
C3	-0.17	**0.70****							
C4	**-0.38****	**0.35****	0.16						
clonal	0.02	**0.38****	**0.52****	**0.27***					
forb	0.00	**0.72****	**0.79****	0.19	**0.59****				
graminoid	-0.14	**0.41****	**0.57****	**0.32***	**0.76****	**0.42****			
legume	0.13	0.10	**0.32***	-0.07	0.21	**0.28***	0.17		
native	**-0.25***	**0.43****	**0.77****	**0.27***	**0.73****	**0.66****	**0.82****	**0.28***	
perennial	-0.14	**0.53****	**0.76****	**0.38****	**0.82****	**0.67****	**0.86****	0.20	**0.92****
short-lived	**-0.30***	**0.47****	**0.50****	0.05	0.07	**0.48****	0.19	0.08	**0.43****
Cover									
Alien	-0.15								
C3	**-0.42****	**0.38****							
C4	-0.08	**0.36****	0.13						
clonal	**-0.27***	**0.45****	**0.40****	**0.53****					
forb	-0.05	**0.74****	**0.34****	**0.46****	**0.49****				
graminoid	**-0.41****	0.23	0.20	**0.39****	**0.48****	0.08			
legume	0.13	0.07	0.02	0.16	-0.15	0.09	-0.08		
native	**-0.57****	0.18	**0.53****	0.17	**0.31***	-0.02	**0.74****	-0.04	
perennial	**-0.54****	**0.39****	**0.60****	**0.24***	**0.48****	0.17	**0.76****	-0.02	**0.87****
short-lived	**-0.36****	0.13	**0.47****	0.02	0.05	0.07	0.05	-0.03	**0.45****

6.3.2 Abiotic parameters

Soils in the study area were medium to heavy clay, with a relatively high pH (7.0–7.9), low electrical conductivity (EC, 0.08–0.27 $dS.m^{-1}$) and low chloride levels (49.2 ± 3.4 $mg.kg^{-1}$) (Appendix F). Cation exchange levels were relatively high (34.6–71.1 $meq.100g^{-1}$), with exchangeable cations in the very high range for calcium and magnesium (31.2 ± 1.3 and 17.2 ± 0.6 $meq.100g^{-1}$, respectively) but moderate to low for potassium and sodium (2.5 ± 0.1 and 0.3 ± 0.1 $meq.100g^{-1}$, respectively). Mean organic carbon was 3.6 ± 0.2%, and nitrogen (nitrate), phosphorus and sulphur levels averaged 9.5 ± 1.2, 164.6 ± 8.6, and 12.9 ± 0.9 $mg.kg^{-1}$ (respectively). Soil pH increased with depth, but levels of other measured variables (EC, nitrate N, OC, phosphorus) decreased relative to surface soil levels (Appendix F).

Differences between distance from tree and topographic position treatments for the surface soil attributes, organic carbon, sulphur and exchangeable sodium were not able to be statistically tested due to non-homogeneous variances (Levene's, $p \leq 0.05$), which could not be corrected by data transformation (Table 6.7). There was no significant interaction between distance from tree treatments and topographic position for other surface soil attributes (2-way ANOVA, $p > 0.05$; Table 6.7).

Shallow soil chloride, cation exchange capacity (CEC), EC, exchangeable calcium and potassium, and phosphorus were significantly higher at 0.5r than at 2r (2-way ANOVA, $p \leq 0.05$ (chloride) and $p \leq 0.005$ (EC and exchangeable potassium); Table 6.7), but there were no significant differences between the 0.5r and 2r distance from tree treatments for pH, nitrate, moisture or exchangeable magnesium cations in shallow soils ($p > 0.05$).

There were no significant differences between topographic position treatments for shallow soil variables, with the exception of exchangeable magnesium cations (2-way ANOVA, $p > 0.05$; Table 6.7), which were significantly higher at Low topographic positions than at High topographic positions (Tukey's, $p \leq 0.05$).

Table 6.7 Differences between distance from tree (0.5r, 2r) and topographic position (low, mid, high) treatments for soil parameters. Treatment values are means and standard error (in parentheses); interaction values are F values. Significant difference is indicated in bold type (2-way ANOVA; ** $p \le 0.005$, * $p \le 0.05$).

Factor	**Distance from tree**		**Topographic position**			**Interactions**
Factor level	**0.5r**	**2r**	**low**	**mid**	**high**	**D x T**
Shallow soils						
Cation Exchnge (meq/100g)	**55.0* (2.4)**	**47.4* (2.0)**	53.4 (2.2)	51.1 (3.9)	49.2 (2.9)	0.24
Chloride (mg/kg)	**57.6* (4.8)**	**40.8* (3.5)**	50.3 (4.9)	56.6 (6.5)	40.6 (5.3)	0.53
EC (dS/m)	**0.19** (0.01)**	**0.13** (0.01)**	0.16 (0.02)	0.16 (0.02)	0.16 (0.02)	0.11
Ex. Calcium (meq/100g)	**34.1* (2.0)**	**28.3* (1.3)**	31.3 (1.5)	30.9 (2.7)	31.3 (2.6)	0.35
Ex. Magnesium (meq/100g)	17.8 (0.9)	16.6 (0.8)	**19.0^{a} (0.9)**	**17.3^{ab} (1.1)**	**15.3^{b} (0.6)**	0.09
Ex. Potassium (meq/100g)	**2.71** (0.09)**	**2.20** (0.10)**	2.53 (0.11)	2.50 (0.20)	2.35 (0.13)	0.11
Ex. Sodium (meq/100g)[4]	0.40 (0.09)	0.27 (0.02)	0.46 (0.14)	0.29 (0.02)	0.25 (0.02)	
Nitrate Nitrogen (mg/kg)[2]	8.5 (1.3)	10.4 (1.7)	7.1 (1.1)	11.1 (2.5)	10.1 (1.6)	1.56
Organic Carbon (%)[1,4]	4.07 (0.26)	3.08 (0.13)	3.41 (0.23)	3.56 (0.37)	3.75 (0.33)	
pH[1]	7.34 (0.06)	7.30 (0.05)	7.26 (0.05)	7.29 (0.07)	7.40 (0.08)	1.50
Phosphorus (mg/kg)[4]	**183.9* (13.0)**	**145.3* (8.7)**	164.3 (10.5)	175.0 (18.0)	154.5 (16.5)	0.18
Sulphur (mg/kg)[4]	14.8 (1.1)	11.0 (1.2)	15.1 (1.7)	12.7 (1.7)	10.9 (0.9)	
Moisture (m^3/m^3)	0.28 (0.02)	0.25 (0.02)	0.24 (0.03)	0.27 (0.03)	0.27 (0.02)	0.07
Deep soil samples						
EC (dS/m)[5]	0.13 (0.02)	0.08 (0.01)	0.06 (0.01)	0.12 (0.02)	0.13 (0.01)	
Nitrate Nitrogen (mg/kg)[5]	1.0 (0.0)	2.6 (1.5)	0.8 (0.3)	2.5 (1.5)	1.5 (0.5)	
Organic Carbon (%)[5]	1.23 (0.14)	1.15 (0.16)	0.85 (0.05)	1.25 (0.12)	1.40 (0.10)	
pH[5]	7.55 (0.14)	7.87 (0.22)	7.93 (0.04)	7.77 (0.23)	7.37 (0.08)	
Phosphorus (mg/kg)[5]	93.8 (18.3)	79.0 (25.7)	35.5 (4.5)	90.3 (16.4)	129.5 (7.5)	
Moisture at 75 cm (dS/m)[2]	0.30 (0.08)	0.27 (0.06)	0.27 (0.07)	0.37 (0.10)	0.23 (0.07)	0.03
Moisture at 150 cm (dS/m)[2]	0.20 (0.02)	0.24 (0.05)	**0.33^{a} (0.07)**	**0.17^{b} (0.02)**	**0.17^{b} (0.01)**	0.55
Other						
Light (incident:ambient)[2]	**0.32** (0.03)**	**0.10** (0.01)**	0.19 (0.03)	0.23 (0.06)	0.22 (0.05)	2.00

[1] arcsin transformed; [2] square root transformed; [3] $\log_{10}$ transformed; [4] heteroscedascity unable to be corrected by transformation; [5] insufficient sample size for analysis by 2-way ANOVA

Differences between distance from tree and topographic position treatments for the deep soil attributes, pH, EC, organic carbon, nitrate and phosphorus were not tested due to small sample size (Table 6.7). There was no significant interaction between distance from tree treatments and topographic position for soil moisture at 75 cm or at 150 cm depths, or for available light (2-way ANOVA, $p > 0.05$; Table 6.7).

No significant differences occurred between the 0.5r and 2r distance from tree treatments for soil moisture at 75 cm and 150 cm ($p > 0.05$); however, there was a significant difference between topographic position treatments for soil moisture at 150 cm ($p \leq 0.05$) with significantly higher levels in the Low treatment, but no significant difference between the Mid and High treatments. Available light at ground level was significantly higher in 0.5r than in 2r distance from tree treatments ($p \leq 0.005$), but did not differ significantly between topographic position treatments ($p > 0.05$, Table 6.7).

Correlations with trees, lippia and floristics

There was a significant negative correlation between canopy cover and available light at ground level (Spearman's, $p \leq 0.005$; Table 6.8). Lippia cover was highly significantly correlated with available light at ground level ($p \leq 0.005$), and significantly correlated with EC, organic carbon, exchangeable potassium and deep soil moisture at 150 cm ($p \leq 0.05$). Lippia reproductive effort was highly significantly correlated with light ($p \leq 0.005$) and the same soil variables (exchangeable K, EC, OC) as lippia cover ($p \leq 0.05$), with the exception of deep soil moisture at 150 cm ($p > 0.05$, Table 6.8).

Table 6.8 Spearman's correlation results for abiotic parameters and (a) tree attributes at 0.5r; and (b) lippia cover (FPC%) and lippia reproductive effort. Values are rho; bold type indicates significant correlation (** $p \leq 0.005$, * $p \leq 0.05$).

	(a) Tree attributes				(b) Lippia attributes		
	n	**Tree height**	**Tree diameter**	**Canopy cover**	**n**	**Lippia cover**	**Lippia reproductive effort**
Cation Exchange	12	-0.09	-0.22	0.46	24	0.21	0.29
Chloride	12	0.03	-0.11	0.16	24	0.27	0.4
Electrical conductivity	12	-0.13	0.22	0.53	24	**0.46***	**0.51***
Exchangeable Calcium	12	0.03	-0.2	0.41	24	0.23	0.31
Exchangeable Magnesium	12	-0.34	-0.26	0.2	24	-0.02	0.06
Exchangeable Potassium	12	-0.14	-0.08	0.54	24	**0.46***	**0.53***
Exchangeable Sodium	12	-0.52	-0.12	0.56	24	0.21	0.31
Nitrate Nitrogen	12	0.15	0.06	-0.2	24	-0.24	-0.33
Organic Carbon	12	0.16	0.2	0.32	24	**0.41***	**0.47***
pH	12	0.39	0.14	0.4	24	0.18	0.16
Phosphorus	12	-0.33	-0.29	0.42	24	0.22	0.23
Sulphur	12	-0.35	0.03	0.54	24	0.24	0.35
Surface soil moisture	12	0.53	-0.02	-0.53	72	-0.02	-0.18
Soil moisture at 75 cm	12	-0.56	-0.17	0.28	72	-0.07	0.07
Soil moisture at 150 cm	12	0.04	-0.09	0.51	72	**0.29***	0.17
Light*	12	0.14	0.1	**-0.60***	24	**0.58****	**0.57****

* proportion of incident:ambient light at ground level

6.4 Discussion

Few studies have investigated the role of facilitation by native species on the success of an invasive species, and the majority of these focus on the establishment phase of the invasion process, and effects on seedling survival (Dunne and Parker 1999, Brooker *et al.* 2008). One of the few studies to investigate facilitation of an invasive species at a range of life stages trialled potential mechanisms by which native chenopod shrubs (e.g. *Atriplex vesicaria*) support the invasive clonal succulent groundcover species *Orbea variegata* in arid-zone South Australia (Lenz and Facelli

2003). None appear to have examined the role of facilitation in the context of multiple species interactions.

This study confirms a close association between lippia abundance and mature *Eucalyptus camaldulensis/E. tereticornis* trees in a grassy riparian woodland at St Ruth Reserve, and suggests that trees facilitate the small-scale competitive advantage of lippia over other (non-lippia) groundcover species in this community. It also indicates that trees play a significant role in the persistence of lippia in the study area in the absence of regular disturbances, and potentially contribute to the ongoing invasion success of this species in both local and downstream environments over time.

6.4.1 Trees as facilitators

Many woody perennial plants exhibit 'nurse'-plant effects which moderate microclimatic conditions and facilitate recruitment of herbaceous species by improving their water status, nutrient content, carbon assimilation rates and growth (Belsky *et al.* 1989, Ludwig *et al*. 2004b, Armas and Pugnaire 2005). Scattered trees can also have significant localised effects on soil properties, creating heterogeneous patches of enhanced soil quality and resource availability (Belsky *et al.* 1993a, Facelli and Brock 2000, Wilson 2002), which may contribute to invasion success under certain conditions (Prober and Thiele 1995). However, Graham *et al.* (2004) report that this effect may be, to some extent, species- and location-specific.

This effect has not previously been reported for either *E. camaldulensis* or *E. tereticornis*, nor has it been tested in a riparian woodland system where nutrient dispersion and environmental heterogeneity are potentially strongly influenced by extrinsic factors such as flooding and catchment runoff processes (Naiman *et al.* 1998, 2005). While broader scale processes such as these can have an over-riding influence on patch-scale heterogeneity and floodplain vegetation community structure and composition (Capon 2005, Turner *et al.* 2004), this study suggests that local within-patch heterogeneity may also be significant in these environments. The greater abundance of lippia in association with trees suggests that such heterogeneity may be an important influence on ecological diversity and ecosystem function which may facilitate alien species persistence (Prober *et al.* 2002a, b) in these systems.

Trees and light

Belsky *et al.* (1989) report a 45–65% reduction in solar radiation, under tree canopies compared to open grassland in a semi-arid east African *Acacia* savanna ecosystem. Light availability under tree canopies in this study was similarly inversely related to canopy cover, with a 51–80% reduction in available photosynthetically active radiation (PAR). However, available light at groundlevel was significantly higher under tree canopies than in the open, canopy-gap areas, where PAR at groundlevel was reduced by 81–94%. This difference was associated with reduced cover of non-lippia species, which included taller-growing perennial grass species such as *Panicum queenslandicum* and *Dichanthium sericeum*, and greater cover of low-growing lippia under trees, and suggests a complex of competitive and facilitative interactions between trees, lippia cover and the cover of non-lippia species.

Cole and Weltzin (2005) report that interactions between different canopy layers can significantly influence light availability and play an important role in determining the competitive relationship between invasive and native species. A closed cover of dominant tussock grass species can limit light availability at ground level and the establishment, survival and growth of lower-growing inter-tussock species (Morgan 1998a). However, shading of this groundcover layer in proximity to scattered trees may disadvantage the dominant C4 floodplain grassland species occurring in the open areas in this study (Sage and McKown 2006), providing opportunities for establishment of more phenotypically plastic C3 (Sage and McKown 2006), but low-growing (Morgan 1998a), species such as lippia.

Trees and shallow soil attributes

Many of the surface soil attributes measured in this study showed consistently high values close to trees, with significant pattern found in a number of these in relation to distance from tree treatments. Shallow soil electrical conductivity (EC) and exchangeable potassium cations showed particularly strong patterns in relation to the presence of trees, while there were also higher levels of chloride, phosphorus, cation exchange capacity (CEC) and exchangeable calcium cations in shallow soils beneath the canopies of mature eucalypts (*E. camaldulensis/E. tereticornis*) than in open areas (canopy gaps) beyond tree canopies. These results largely conform with the findings of other studies, across a range of ecological communities both in Australia and elsewhere, which have variously reported elevated levels of total carbon, total nitrogen, available phosphorus, exchangeable cations, pH and electrical conductivity associated with scattered trees (e.g. Tongway and Ludwig 1990, Belsky *et al* 1993a, b, Hastwell 2001, Jackson and Ash 2001, Prober *et al.* 2002 a, b, Wilson 2002, Graham *et al.* 2004, Wilson *et al.* 2007).

Levels of nitrate N, sulphate S, pH, organic carbon (OC), cation exchange capacity (CEC) and exchangeable magnesium cations in this study were comparable to those previously reported for similar cracking clay soil types (uncropped, cropped) on the Darling Downs and more generally in the northern Murray-Darling Basin (e.g. Conteh *et al.* 1997). Phosphorus concentrations (104–258 $mg.g^{-1}$) were considerably higher than previously reported for the northern Murray-Darling Basin (5–78 $mg.g^{-1}$), including the Darling Downs (8–40 $mg.g^{-1}$) (Conteh *et al.* 1997). Maximum levels of exchangeable potassium and calcium cations were 2.0 and 1.5 times, respectively, the highest values previously reported for the Darling Downs by Conteh *et al.* (1997), while levels of exchangeable sodium were relatively low at only 40% of previously recorded levels for the region (Conteh *et al.* 1997). These values may in part be due to the stratified design in this study which entailed sampling closer to trees than would be the case in a random design. They may also be a function of the riparian location, which many studies have previously noted as areas of relatively high nutrient status due to catchment runoff processes (Griffiths *et al.* 1997, Tabacchi *et al.* 1998). High calcium and low sodium salt levels have been previously attributed to the calcic geological foundation of cropping soils in the Condamine catchment (Shaw *et al.* 1994).

Higher levels of chloride and electrical conductivity (hence salinity, as defined by Shaw 1999) closer to trees than in canopy gaps concur with patterns reported by Prober *et al.* (2002a,b), Munzbergova and Ward (2002), and Eldridge and Wong (2005). Trees have been noted for their influence on localised salt accumulation and distribution patterns resulting from shallow groundwater uptake and salt exclusion by tree roots at the capillary fringe (Nosetto *et al.* 2007). In the Negev Desert, this results in potential trade-offs for species growing in under-canopy environments, which need to balance the positive effects of higher nutrient levels against the negative impacts of higher soil salinity (Munzbergova and Ward 2002). However, this is unlikely to be an issue for the majority of species in the study landscape where salinity ratings (Shaw 1999) were relatively low.

Higher levels of exchangeable cations in association with trees have also been reported previously. Gomez-Aparicio *et al.* (2005) report increased levels of potassium cations in soils beneath dominant tree species grown in experimental plots in Spain. Prober *et al.* (2002a) also found higher levels of available potassium beneath trees than in open areas in temperate grassy woodland communities in southeastern Australia.

While correlations between surface soil attributes and tree and canopy dimensions were not statistically significant in this study, possibly due to the limited sample size (hence low power of the analyses), higher correlations between some surface soil attributes (e.g. exchangeable sodium cations, soil moisture) and tree height or canopy cover suggest that the attributes of individual trees may be important in determining the level to which resources are accumulated and soil attributes are modified by scattered trees in woodland situations. Allometric relationships signify that larger trees are also likely to have larger root systems, capable of drawing resources from a greater volume of soil (Scholes and Archer 1997, Peichl and Arain 2007). Greater canopy cover is also likely to indicate a tree which is larger and healthier, more active in accessing resources and with more active process contributing to below-canopy litter accumulation (Scholes and Archer 1997, Prescott 2002). Higher nutrient levels under older trees have also been attributed to length of residency, but may not be apparent until trees reach a critical age or size (Scholes and Archer 1997).

Trees and soil moisture

Studies conducted under average rainfall conditions have shown a distinct depression in soil water content in the presence of trees (e.g. Belsky *et al.* 1989, Fensham and Fairfax 2007, Huth and Poulton 2007, Nosetto *et al.* 2007). Lack of significant patterning in soil moisture content in relation to the presence of trees in this study suggests that water availability in the study area was depleted at the time of sampling, presumably as a result of prolonged drought (e.g. Belsky *et al.* 1989).

Patterns in soil moisture appear to have been more closely associated with the attributes of individual trees. Positive and negative correlations for canopy cover and tree height with shallow and subsoil moisture levels indicate potentially complex interactions between the hydraulic function of trees and competitive effects of neighbouring plants as was found by Ludwig *et al.* (2003, 2004a,b), rather than amelioration of under-canopy groundcover evapotranspiration as reported by Belsky *et al.* (1993a).

6.4.2 Lippia response to environmental conditions

Lippia and light

In the current study, lippia showed a strong association with the amount of available light at ground level. While it appears counter-intuitive, this was higher beneath the canopies of trees in this study (which had an average cover of 23.5%, providing only light dappled shade and high levels of sun-flecks; Sage and McKown 2006) than in canopy gaps, where cover of taller non-lippia herbaceous vegetation, dominated by perennial graminoids, reduced light availability at ground level by up to 94%. This is also supported by the observed change in lippia growth habit from a densely rooted matting form beneath trees to a loosely trailing exploratory form amongst other groundcover species. This exploratory type of growth is related to the density and height of neighbouring species (Taylor and Ganf 2005, Chen *et al.* 2010), and is a response to limited resource availability (Slade and Hutchings 1987, Chen *et al.* 2010), and increased competition for light (Taylor and Ganf 2005, Xu *et al.* 20010b).

Lippia's requirement for a high light environment is supported by findings from a glasshouse trial investigating lippia response to full sun and reduced light (85% shade) conditions (Xu *et al.* 20010b). In that study, significant light-sensitive declines in leaf nitrogen (area-based), photosynthetic nitrogen use efficiency, chlorophyll to nitrogen ratio, and nitrogen stable-isotope signature occurred in lippia ramets (daughter plants) grown in reduced light conditions where these were isolated/separated from the genet or mother plant. This response was eliminated in shaded ramets which remained connected to the mother plant growing in full sun. This trial indicated not only the reduced performance of lippia under low light conditions, but also the importance of clonal integration in maintaining access to essential resources (Xu *et al.* 20010b).

Lippia and shallow soil attributes

The current study indicates a significant relationship between lippia cover and reproduction and a range of surface soil attributes. Most significant of these was the concentration of exchangeable potassium cations, cation exchange capacity and organic carbon content. Cation availability and relative concentrations are recognised as important drivers of plant performance in agriculture (e.g. Oborn *et al.* 2005), but are rarely considered in native vegetation ecosystems although their potential role in the assembly of multi-species communities on low-fertility serpentine soils in the US has been suggested (Moore and Elmendorf 2011). Higher potassium levels have been found elsewhere to contribute to increased drought tolerance through increased plant water use efficiency (Egilla *et al.* 2001); for example, higher levels in soils under nurse shrubs in the Mediterranean were associated with improved seedling performance (Gomez-Aparicio *et al.* 2005). The strong association between lippia and available potassium cations in this study has not been reported previously. Xu and van Klinken (2008) report consistently higher calcium levels in lippia leaf tissue than in the pasture grass species tested, and interpret this as a potential herbivore defence in lippia, but potassium levels are not reported.

A strong association between lippia cover and organic carbon levels is apparent in this study, but has also not been reported elsewhere. Xu and van Klinken (2008) do not report organic carbon levels, but found altered soil carbon isotope ratios under lippia infestations. At the most heavily infested site, organic carbon 13C, typical of C4 grasslands (Boutton *et al.* 1999), was significantly depleted and up to 70% of the surface soil organic carbon pool had been substituted as a result of lippia invasion (Xu and van Klinken 2008). Altered carbon isotope ratios contribute to changes in soil microbial activity and communities (Ehrenfeld *et al.* 2001, Kramer and Gelixner 2006), and potentially facilitate the competitive success of invasive species, as has been reported for spotted knapweed *Centaurea maculosa* in native prairie ecosystems in north-western USA (Carey *et al.* 2004).

Limited patterning in nitrate levels in relation to trees in this study, as well as limited association between lippia and nitrate, appears to indicate that this component of available nitrogen is either not limiting in this environment or that accumulated nitrate under trees is rapidly acquired by lippia (e.g. Clech-Goods 2010). In grassy eucalypt woodlands, Prober *et al.* (2002a) found no relationship between nitrate concentration and the presence of trees, although nitrate levels were relatively lower in that study (ranging from 0.1–1.8 mg.kg^{-1} compared to a range of 2.0–24.0 mg.kg^{-1} in the current study). Prober *et al.* (2002a) suggested that available nitrogen (nitrate, ammonium) patterns may be governed by the nitrogen uptake efficiency of the vegetation, including alien annuals which were found to be linked to rapid recycling of available nitrogen in that system. Xu and van Klinken (2008) found lower nitrate-based nitrogen in soils under lippia infestations compared to non-lippia invaded pastures in eastern Australia, as well as low C:N ratio in lippia leaf material suggesting that lippia litter would be rapidly decomposed (Zhang *et al.* 2008).

Significant changes in soil nutrient attributes (nutrient dynamics, stable isotope signature) have been reported under lippia infestations in invaded pastures in eastern Australia (Xu and van Klinken 2008). In addition to lower nitrate nitrogen concentration, invaded soils had lower pH and higher EC than non-invaded soils under either native or improved pasture (Xu and van Klinken 2008). While there was no apparent patterning in pH levels in this study, higher EC under tree canopies at 0.5r, as well as significant correlation of lippia cover with EC, indicates that lippia could be an active contributor to this pattern.

Lippia and soil moisture

Lippia is renowned for its capacity to significantly reduce soil moisture content (Lucy *et al.* 1995). Significant changes in soil moisture under lippia infestations were confirmed by Xu and van Klinken (2008), who reported a 16–39% reduction in invaded soils compared with neighbouring uninvaded native grasslands and improved pastures in eastern Australia. In the current study, there was no significant association between shallow soil moisture content and lippia cover, and a relatively weak correlation between lippia cover and deeper soil moisture at 150 cm depth. This depth is below the reported maximum rooting depth (around 70 cm) of lippia (Taylor and Ganf 2005), although Ludwig *et al.* (2004b) report increased rooting depth in plants associated with trees where hydraulic lift occurs. This is interpreted as a response to increased competition between trees and neighbouring vegetation in semi-arid regions (Ludwig *et al.* 2004a). Lippia's close association with deep-rooted trees capable of hydraulic redistribution in the study area suggests that this may be an important process which potentially contributes to the success of lippia in this landscape by facilitating the species' persistence through drought periods. However, this requires further investigation as neither groundwater depth nor tree condition were found to be strong predictors of lippia abundance on the Upper Condamine floodplain in the study reported in Chapter 5.

The significant association between lippia cover and organic carbon levels under tree canopies may contribute to better soil moisture relations, benefiting lippia under tree canopies during drought conditions (Belsky *et al.* 1989, 1993a), although this is not reflected in significant surface soil moisture differences in this study.

6.4.3 Vegetation responses to lippia

In the current study, gradients in floristic composition were strongly associated with lippia abundance (cover); however, these were also apparent in relation to distance from, or proximity to, trees. While correlations between trees and lippia cover represent a potentially confounding influence on floristic composition in these communities, response to the presence of trees was most apparent in terms of variation in the cumulative cover of non-lippia species and, to a lesser extent, community diversity, both of which increased significantly with distance from trees. In contrast, species richness was not significantly influenced by the presence of trees.

Lippia cover, independent of proximity to trees, was significantly negatively correlated with the abundance of co-occurring floristic species, including abundance within functional groups. This appeared to be particularly so where percentage cover of lippia was greater than 20%. Decline in species richness with increasing cover and dominance of lippia was also evident but more gradual. These findings are consistent with those reported from other research into the impact of invasive species on community composition. In a systematic review of studies which investigated the community level impacts of 13 invasive 'neophytes' (novel plant species) in the Czech Republic. Hejda *et al.* (2009) found that, for individual invasive species, impacts on species richness, community evenness and diversity were driven predominantly by the ability of that species to monopolise space, confirming the suggestion by Gordon (1998) that highly invasive species which become dominant are most likely to have significant impact.

In the current study, lippia was significantly more dominant than any other species. Of the 44 species recorded, it was both the most frequently recorded (being present in 96% of the 72 sample quadrats) and, on average, the most abundant with a mean cover of 28%. The cover of lippia was, on average, 61% greater than the next most abundant species and most dominant native species in these communities, which was the native perennial grass *Paspalidium distans*, occurring in 76% of samples with a mean cover 11%. Hejda *et al.* (2009) found that impacts on community diversity were greatest where the cover of the invasive species was at least 47% higher than that of the next most dominant species. On this basis, the relative dominance of lippia in this study indicates its potential for significant impact on the floristic composition of the riparian woodland community at St Ruth Reserve.

Hejda *et al.* (2009) also suggest that invasive species are more likely to attain dominance, in terms of the cover and homogeneity of the stand, where the native community comprises many competitively weak native species. Weak competitive interactions are potentially the case in dryland floodplain communities where species are adapted to both drought and flooding disturbance, and in moderately grazed native pastures favouring high species diversity (Olff and Ritchie 1998). In theory, many of these should be species which are better adapted to coping with disturbance and related abiotic stresses, including ruderal species capable of rapid establishment, growth and reproduction following disturbance, than species which are adapted for competition (Grime 1977, 2007). Hejda *et al.* (2009) also suggest that changes in species composition following invasion usually result in an increase in resistant ruderal species. It is not feasible to test this hypothesis in the study landscape, where few, if any, pristine remnants exist and lippia has been present (and possibly prolific) for up to 80 years (i.e. it is a universally disturbed, lippia-invaded landscape). However, in this study, of the 33 species recorded across 26 (of 72) quadrats with lippia cover of 25% or more, 21 species were still present in the ten quadrats with lippia cover of 80% or more, indicating a relatively large pool of resistant species, including the native grasses, *Paspalidium distans* and *Elymus multiflorus*.

There appears to be a 2-phase relationship between lippia cover and the cumulative cover of non-lippia species, with a more variable response where lippia cover is less than 20% and greatly reduced variability in the cover of non-lippia species where lippia cover exceeded 20%, indicating a possible threshold above which lippia exerts a significant impact on floristic composition and community structure. Gooden *et al.* (2009b) found a similar 2-phase response to lantana (*Lantana camara*) cover, with a sudden decline in native species richness at 75% lantana cover. Taylor and Ganf (2005) report a stepped response in lippia cover (i.e. interpreted as an invasion threshold for lippia in relation to the presence of existing plants), under experimental conditions, where the stand density of the native grass species *Sporobolus mitchellii* was 25% and above; although, stand densities tested in this study were 0, 25, 50, 75 and 100% of 36 (4 x 4 cm) cells within planter boxes, and it is unclear how this relates to projected foliage cover under field conditions.

6.4.4 Lippia-tree interactions and ecosystem condition/function

Previous studies have found that lippia, a low-growing clonal species, is able to rapidly pre-empt space where taller growing native species cover is significantly reduced by grazing or flooding, but that repeated disturbance may be required for lippia to maintain this competitive advantage (Price *et al.* 2008, 2010a, 2011). While lippia abundance at the study site is a legacy of extensive infestation associated with the previous heavy grazing regime, localised high-abundance lippia ‘populations’ remain, despite limited disturbance and significant recovery of non-lippia groundcover over much of the area in recent years.

The results of this study, which indicate that lippia persists in the study area in the absence of ongoing disturbance, supports a new interpretation which incorporates the potentially dynamic relationship between tree canopy cover, lippia cover and the cover and diversity of non-lippia species in lippia-infested riparian woodlands. Key interactions suggested by this study are summarised in Figure 6.7. While mechanisms were not investigated, evidence of strong correlation with abiotic and community response variables is interpreted as significant influence within the context of this study. In summary, dappled light conditions under tree canopies drive a negative response in C4 perennial tussock grasses, the dominant ‘non-lippia’ herbaceous species, resulting in reduced cover of tall groundcover species and higher relative light availability at groundlevel under tree canopies in this landscape. This confers a competitive advantage to lippia, a light-dependent C3 species which may also benefit from differential under-canopy soil attributes, including higher levels of certain soil nutrients and soil moisture (Xu and Van Klinken 2008, Xu *et al.* 2010b), under trees. Consolidated (abundant densely rooted) lippia growth in response to differential resource availability may act to further exclude non-lippia species at this spatial scale.

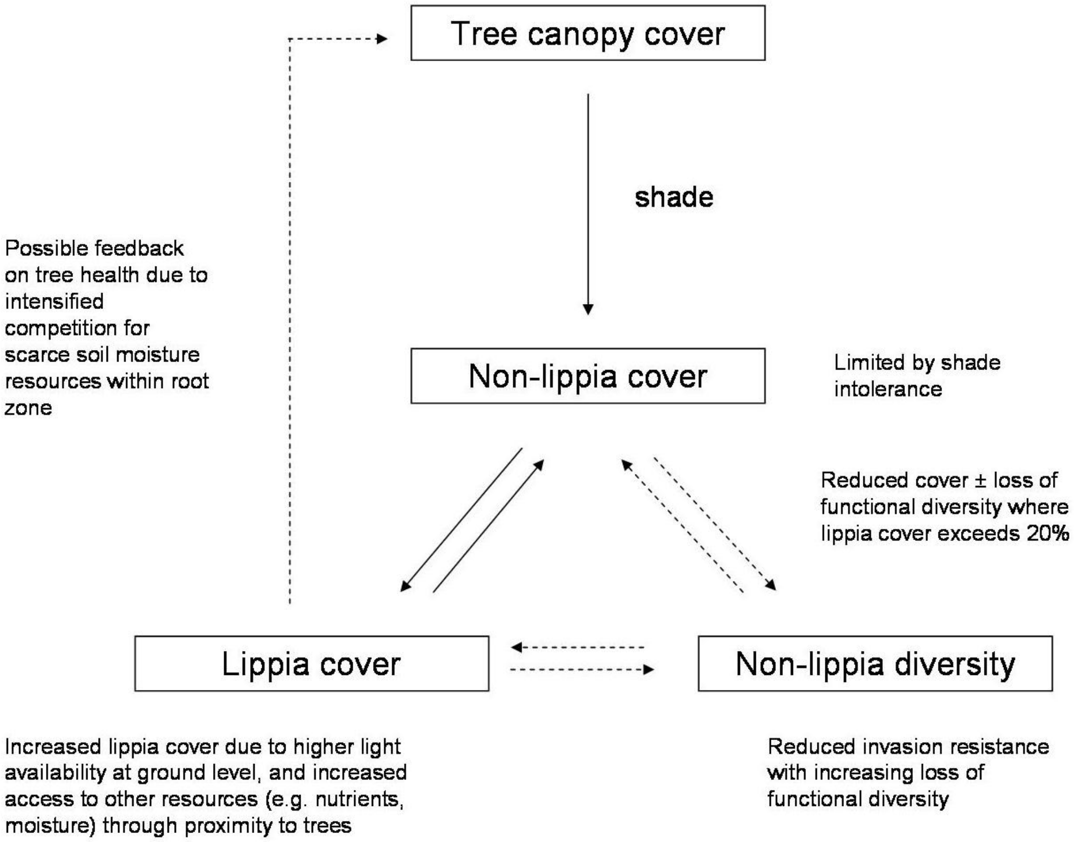


Figure 6.7 Conceptual diagram of interactions and potential feedbacks between canopy cover, and cover of lippia and non-lippia (predominantly C4) vegetation. Solid lines show the key relationships and directions of influence indicated by this study; dotted lines indicate relationships which are suggested but require further investigation.

Weaker associations and potential feedbacks which require further investigation are also indicated in Figure 6.7. Other studies report that established lippia populations can act as a base for rapid localised vegetative expansion of lippia under conditions of spatially and temporally variable resource availability (Price *et al.* 2011). Well-resourced patches of lippia also support ramet growth and infiltration into more hostile areas (Xu *et al.* 2010b) in response to changes in the cover and density of neighbouring non-lippia vegetation with disturbances such as grazing, drought or flooding (Taylor and Ganf 2005, Berney *et al.* 2010, Price *et al.* 2010a, 2011). While such expansion may be only temporarily successful, it may have a long-term impact on the diversity of native species which historically establish under suitable conditions in inter-tussock spaces in this environment (Table 6.6). This study suggests that changes in the diversity and structure of groundcover vegetation may further constrain the capacity of non-lippia vegetation to resist lippia infiltration. The outcome of competitive interactions may also vary temporally in response to changes in tree canopy cover or tree health, while seasonal changes in shade distribution around trees may also be important at this scale (e.g. Belsky *et al.* 1989). In addition, the capacity for high lippia levels to alter soil and moisture conditions (Xu and Van Klinken 2008) also indicates the potential for competition and feedback influences on tree health under conditions of resource scarcity. These are discussed in more detail below.

6.4.5 Significance and limitations

This study is the first to investigate the role of canopy trees in facilitating the abundance and persistence of the invasive alien groundcover species lippia *Phyla canescens* in remnant floodplain riparian woodlands in the absence of grazing or flooding disturbance. It suggests that trees may play a significant role in mediating small-scale interactions between lippia and non-lippia vegetation through their impact on local levels of resource availability. In this study, while lippia prevalence at the study site was a legacy of historical over-grazing, a key correlate of current lippia abundance, hence its ability to remain dominant over non-lippia vegetation, was the availability of light at ground level, which was higher under *E. camaldulensis/E. tereticornis* canopies than in canopy gaps due to the impact of dappled shade on the cover of non-lippia species. Reduced cover of taller growing non-lippia herbaceous vegetation (e.g. perennial tussock grasses) and increased light at ground level enable lippia to consolidate its growth and maintain a high level of abundance (up to 100% cover) in association with trees. This study also suggests that soil organic carbon and exchangeable cations may play an important role in lippia's success in this landscape.

Strong association with trees in this landscape also has implications for the future spread of lippia. The prevalence of strongly rooted highly integrated consolidated lippia growth under tree canopies in this study indicates potential for rapid local expansion of lippia from these refugia with a return to suitable conditions. Rapid extension and rooting of new ramets in bare soil, supported by clonal integration with established plants (Xu *et al.* 2010b), gives lippia a temporal advantage over species which rely solely on recruitment from the soil seedbank, and an increased probability of successful establishment (Price *et al.* 2011). Lippia infestations can expand locally by this mechanism, particularly where disturbance has resulted in low cover and density of non-lippia species (Price *et al.* 2010a, 2011). The ability to maintain healthy populations may also provide a significant advantage and future benefit to lippia's success, both locally and in the wider landscape. High lippia cover is correlated with high reproductive effort (flowering and seed production) in this study, indicating that trees may also facilitate ongoing contributions to the persistent soil seedbank in this environment, despite adverse climatic conditions. Propagule pressure is a primary driver of invasion success (Colautti *et al.* 2006), and a substantial soil seedbank in source populations represents a significant risk to downstream environments with subsequent dispersal in floodwaters (Stokes *et al.* 2007, 2008, Macdonald 2008). A high level of sexual reproduction in Australian lippia populations has also been linked to a capacity for rapid micro-evolution, increasing lippia's ability to succeed under highly variable climatic conditions (Xu *et al.* 2010a).

Heterogeneous cover of lippia in these woodlands, and indication of association with a small number of key resources, suggests the potential for strategic management of lippia through the manipulation of resource availability (e.g. light, levels of exchangeable cations such as potassium) on the relatively small tree-based scale. Manipulation of key resources has been used effectively in small-scale trials elsewhere (e.g. Prober *et al.* 2005). Xu *et al.* (2010b) have shown lippia's growth and productivity dependence on high light availability, and capacity to manipulate this. However, while this current study indicates association between some resources and lippia abundance and reproduction, these results are correlative only and not indicative of causality. Further research is required to determine the potential and cost-effectiveness of manipulating resource availability or specific soil attributes to control lippia.

Other studies have indicated that available soil moisture may also be important to lippia (Taylor and Ganf 2005, Price 2011), but this was not apparent in this study where limited variation in soil moisture levels in both surface and subsoils due to drought conditions may have masked the potential importance of water availability to lippia in this landscape. Hydraulic lift is undoubtedly an important process in the vegetation type, however broadscale changes occurring across the Upper Condamine floodplain indicate chronic groundwater decline in the general study area (Chapter 2). Data from monitoring bores within 5 km of the St Ruth reserve indicate that mean groundwater levels were at 18.4 m in 2004–05 and declining at an average rate of 1.8 m per decade (DNRMW 2008). As a result, it is likely that the roots of trees sampled in this study have limited connectivity with shallow groundwater resources and that hydraulic lift processes may not operate effectvely. This implies increasing reliance on stochastic rainfall events (e.g. Elmore *et al.* 2003, 2006a) and increased potential for hydraulic failure under extended drought conditions (Tyree and Sperry 1988, McDowell *et al.* 2008). Lippia is reported to be capable of significantly depleting soil moisture (Lucy *et al.* 1995, Xu and Van Klinken 2008), and its close association with trees in this landscape indicates that intense competition for scare surface soil moisture may occur, exacerbating moisture stress and potentially contributing to reduced hydraulic function in ‘host’ trees.

In a study conducted by Ludwig *et al.* (2004a), increased competition between trees capable of hydraulic lift and neighbouring herbaceous vegetation for surface soil moisture resulted in no net benefit to trees. A similar effect between lippia and host *Eucalyptus camaldulensis/E. tereticornis* may represent additional pressure on tree health in this landscape, particularly under conditions of severe water deficit, compounding the impact of significant groundwater decline in the study landscape. However, further investigation is required to identify the water sources used by trees and lippia, and to determine whether, and under what conditions, the relationship between these two species, in terms of water relations, is primarily facilitative or competitive.

Lack of significant patterning between topographic position treatments, of lippia cover and all environmental variables except subsoil moisture, indicates that microtopographic refugia, if important, may work independently of tree-based refugia in this landscape. This is reinforced by the limited interaction found in this study between distance from tree and topographic position. Alternatively, the range of positions chosen in this study may not have captured the location of active microtopographic refugia still operating under the dry climatic conditions at the time of sampling; the role of these in supporting localised high density lippia populations may require further investigation.

This study is also the first to investigate small-scale interactions between lippia and non-lippia species in invaded remnant native vegetation communities in Australia. Results indicated a potential threshold impact level of lippia infestation at around 20% cover, up to which non-lippia vegetation exhibited a variable response to lippia invasion and beyond which the cover of non-lippia species declined rapidly. While this response requires further investigation, it indicates a direct (possibly non-linear) impact on floristic composition and community structure, and the potential of this invasive species to alter the functional diversity and dynamics (including resilience) of invaded communities where lippia cover is not maintained below this level.

It is unclear whether the results of this study can be applied to other landscapes in which lippia is currently absent and in which grazing does not occur. Initial establishment of lippia in the study area was most probably associated with a combination of historical flooding and grazing disturbance regimes prevalent both within upstream riparian communities and locally within the St Ruth reserve. It is also possible that the previous history of the study area as a livestock camping and watering reserve, and more recently as a heavily stocked leased grazing area (Chapter 2), may have contributed to the observed patterning in some measured soil attributes (Marshall 1974, Taylor *et al.* 1985, Lunt 2005); for example, physical disturbance, compaction and resource accumulation in stock camps under trees may have contributed to the inital loss of native shade-tolerant C3 species (Allsopp *et al.* 2007) and lippia establishment and consolidation in these locations. While grazing exclusion, in combination with extended drought, has resulted in a significant decline in lippia cover and a corresponding increase in the cover of native species at St Ruth Reserve (QMDC 2005), lippia continues to be a dominant component of the groundcover vegetation, indicating that the legacy of past disturbance persists in the study area. However, persistent high cover of lippia under tree canopies appears to be less related to ongoing disturbance, such as grazing and flooding, than to pre-emption and consolidation of occupied space under abiotic conditions which confer a competitive advantage to lippia over co-occurring native species.

6.5 Conclusion

This study investigated interactions between dominant canopy trees and lippia in remnant riparian *E. camaldulensis/E. tereticornis* woodlands, as suggested in the analysis of environmental drivers of community pattern reported in Chapter 5. It found a positive association between mature canopy trees and lippia cover, reproductive condition and growth habit, and indicated that trees influence small-scale heterogeneity in floristic composition (community structure) and, in particular, the strength of interactions between lippia and non-lippia species. Scattered trees in this study appeared to confer a competitive advantage to lippia over neighbouring non-lippia groundcover species, mediating interactions between lippia and non-lippia species through their influence on resource availability and environmental conditions. Consolidated refugial populations, such as those persisting in a ‘halo’ around the base of mature trees, continue to flower and contribute seed to the soil seedbank during drought, representing a significant risk to downstream areas with low groundcover with subsequent flooding. These persistent refugial populations also represent secure sites from which lippia can rapidly expand locally through vegetative growth with the return of favourable conditions such as above-average rainfall and the reintroduction of grazing.

Environmental variables, influenced by the presence of trees and associated with high lippia cover and reproduction, included high levels of available light at ground level, and elevated levels of exchangeable cations, particularly potassium, and soil organic carbon which may contribute to higher drought tolerance in this mesic C3 species. It is suggested that further research is required to establish mechanisms and thresholds for lippia response to key abiotic gradients, as a foundation for strategic control in remnant ecosystems.

The absence of any significant local soil moisture gradient in relation to the presence of trees was unexpected, but potentially influenced by drought conditions at the time of sampling and reduced access to declining shallow groundwater resources in this highly modified landscape. However, there is potential for strong competitive interactions for scarce water resources between abundant densely rooted lippia populations and their host trees which may compound localised soil water deficits, reinforce tree dieback responses and exacerbate woodland decline where groundwater levels are no longer accessible to deep tree roots. This may be the case in sections of the Upper Condamine where groundwater extraction has contributed to widespread chronic groundwater decline, as outlined in Chapter 2.

The next chapter synthesises the results from this and previous chapters into a conceptual state and transition model of riparian woodland response on the highly modified Upper Condamine floodplain. Rather than a discrete ecological model, Chapter 7 also incorporates the socio-ecological context of these woodland ecosystems to develop a holistic model which explores the drivers/attributes operating in this complex highly modified production landscape.

Chapter 7 A conceptual state and transition model for Upper Condamine floodplain riparian woodlands

7.1 Introduction

A primary objective of sustainable management is to maintain the resilience of ecosystems and their ability to respond and adapt to future disturbances and change (UNEP 2009). This can only be realistically achieved on the basis of an understanding of the relationships between disturbance, ecosystem pattern and underlying ecological processes. The broader socio-ecological context of ecosystems in production landscapes, where sustainable land management encompasses biodiversity conservation and continued ecosystem service provision in systems subject to significant anthropogenic change, adds an additional level of complexity to this understanding (Walker *et al.* 2002). Native ecosystem remnants embedded in highly modified landscapes are subject to altered disturbance regimes and degradation pressures which potentially shape their composition, structure, ecological function and resilience to future disturbance (Walker and Meyers 2004, Walker *et al.* 2006).

Conceptual models are valuable tools which aid in the definition and exploration of important relationships between key components of complex systems (Gentile *et al.* 2001, Spooner and Allcock 2006). They provide an effective framework for summarising and communicating current knowledge based on empirical evidence and also a means of incorporating theoretical understanding of the function and behaviour of an ecosystem. They can effectively extend existing knowledge, which in many cases may be limited, and provide a framework within which critical gaps in knowledge and understanding of a system can be identified. In this way, they can contribute to the development of hypotheses regarding system responses to, and future outcomes of, environmental change including management actions (Yates and Hobbs 1997, Gentile *et al.* 2001, Spooner and Allcock 2006). They can also provide valuable links between both theoretical and empirical research (Herrick *et al.* 2006), and between research and ecosystem management (Spooner and Allcock 2006).

This chapter develops a conceptual ecosystem response model for riparian woodland communities on the Upper Condamine floodplain, based on evidence derived from this study and a review of the relevant literature. Research reported in this thesis indicates multiple drivers of composition, function and condition in remnant woodlands in this highly modified production landscape. The model proposed in this chapter incorporates those factors which drive critical transitions between alternative stable states in these woodlands.

7.1.1 Conceptual models and ecosystem dynamics

Native disturbance-driven ecosystems exhibit both equilibrium and non-equilibrium dynamics (Briske *et al.* 2003, Stringham *et al.* 2003). Continuous and reversible vegetation dynamics are evident within dynamic stable states controlled by a particular set of stabilising feedbacks (i.e. the governing stability regime) (Stringham *et al.* 2003, Briske *et al.* 2008). Disturbance within the historical range (i.e. the adaptive/evolutionary disturbance regime) essentially resets the position of a given vegetation patch along the successional trajectory, while spatial variability in the occurrence and intensity of disturbances contributes to beta diversity and a dynamic patch mosaic of ecosystem state phases, though not necessarily alternative stable states, within a landscape unit (Stringham *et al.* 2003, Briske *et al.* 2008). Transitions between state phases within a stability regime are linear and reversible (Fuhlendorf *et al.* 2001, Stringham *et al.* 2003). Such dynamics are captured in the traditional climax, equilibrium or ‘range’ model of community development (Briske *et al.* 2003).

Non-equilibrial system dynamics are conceptualised in ‘state and transition’ model frameworks (Westoby *et al.* 1989) which recognise the potential for alternative stable states and accommodate discontinuous (non-linear) and non-reversible vegetation change between these (i.e. polyclimax theory; Tansley 1935, Whittaker 1953). Alternative stable states operate under different stability regimes (i.e. sets of stabilising feedbacks), and transitions between these involve the crossing of critical biotic and/or abiotic thresholds (Stringham *et al.* 2003, Briske *et al.* 2003, 2008). Such critical transitions may be fast or slow, but transition back to a previous alternative state is improbable without active management and significant input (Friedel 1991, Prober *et al.* 2005, Stringham *et al.* 2003).

Early use of the state and transition framework was confounded by lack of recognition that both equilibrium and non-equilibrium dynamics may occur in ecosystems (Briske *et al.* 2003, 2005). In addition, disturbance history may significantly influence observed response dynamics. For example, reversible (linear) shifts in floristic composition are apparent in response to changes in grazing intensity in systems with a long evolutionary history of grazing and where resilience mechanisms to this type of disturbance have evolved; irreversible transitions and alternative stable states (i.e. non-equilibrial dynamics) are more likely in systems where grazing is a novel disturbance to which resilience mechanisms are not fully developed (Cingolani *et al.* 2005a). These issues have been resolved to some extent by clarification of terminology and better definition of model terms (Stringham *et al.* 2003), and by increasing empirical evidence and understanding of the behaviours of complex ecosystems (e.g. Cingolani *et al.* 2005a, Colloff and Baldwin 2010). Concurrent development of resilience theory has led to greater recognition of the value of the state and transition approach in effectively conceptualising elements of ecosystem resilience and change (Briske *et al.* 2006, 2008). At the same time, research into the role of plant functional traits in vegetation community dynamics provides an important mechanistic link between vegetation change and ecosystem function, which can also be represented within the state and transition framework (McIntyre and Lavorel 2007).

State and transition models

The state and transition modelling framework (Westoby *et al.* 1989) is based on the theoretical concept of non-equilibrial ecosystem dynamics and resilience. This theory effectively proposes that different successional trajectories are possible within a landscape unit, and that ecosystems can be expressed as a number of alternative stable (resilient or resistant) states separated by transitions from one stability regime to another in response to environmental change (Holling 1973, Walker *et al.* 1999, Gunderson 2000, Chapter 1). Resilience theory proposes that a stable state is maintained by negative (stabilising) feedbacks which reinforce the current state (Peterson *et al.* 1998, Briske *et al.* 2006, 2008), while change between states involves a ‘switch’ from these to positive feedbacks (‘feedforwards’) which initiate, and frequently accelerate, change (Suding *et al.* 2004, Hagerthy *et al.* 2008). Transition between states may involve specific thresholds in biotic and/or abiotic conditions, with shifts across these (and between states) driven by natural events (e.g. succession, disturbances) and/or human activities (e.g. land use change, management) (e.g. Scheffer *et al.* 2001, Scheffer and Carpenter 2003, Suding and Hobbs 2009). Such ‘critical’ transitions may be triggered by climatic extremes (Parmesan *et al.* 2000, Scheffer *et al.* 2001, Walther *et al.* 2002) or large infrequent disturbances (Turner *et al.* 1998), acting independently or in combination (Briske *et al.* 2008, Raffa *et al.* 2008). Transitions are often non-linear, and potentially difficult to reverse, with unpredictable outcomes due to the complexity of factors involved (Scheffer and Carpenter 2003, Suding and Hobbs 2009).

Initially developed as an alternative to the range succession model, which assumed linear reversible change, in grazing rangeland management systems (Westoby *et al.* 1989), state and transition models (STMs) have gained wide acceptance as tools for representing non-linear ecosystem responses to change, particularly where this is management-induced (Stringham *et al.* 2003). STMs provide a framework for organizing current understanding of ecosystem dynamics; information about potential alternative states can be graphically arranged (as box and arrow diagrams, with boxes representing states and phases within states and arrows representing transitions) in order to clarify relationships between these. Originally based on states defined by dominant indicator pasture species (e.g. Stockwell *et al.* 1994, Phelps and Bosch 2002), STMs have since been developed to incorporate a comprehensive range of ecosystem components relating to ecosystem structure and ecological function (e.g. Stringham *et al.* 2003, Briske *et al.* 2008). STMs are now applied widely across a range of management contexts and ecosystem types subject to transition due to natural or anthropogenic disturbance, including:

- the management and restoration of endangered eucalypt woodlands (Yates and Hobbs 1997, Prober *et al.* 2002b, Spooner and Allcock 2006);
- threshold responses to secondary salinity in southern Australia (Cramer and Hobbs 2005);
- post-mining rehabilitation to a self-sustaining jarrah forest ecosystem in Western Australia (Grant 2006);
- impacts of grazing, fire and climate impacts on carbon dynamics in Australian savannas (Hill *et al.* 2005), and of natural disturbances and fire management in the upper Grande Ronde Sub-basin of northeast Oregon (Hemstrom *et al.* 2007);

- response in plant traits to changes in soil resource availability and disturbance regimes associated with changing grassland management in subalpine grasslands in the central French Alps (Quetier *et al.* 2007).

A set of concise definitions for state-and-transition model components was developed by Stringham *et al.* (2003). This has contributed to greater clarity in the development of STMs, which increasingly encompass factors which govern the resilience and resistance of an ecosystem's primary ecological processes, hence ecosystem stability. These include abiotic factors relating to landscape function (Tongway and Hindley 2004), such as hydrology and soil characteristics (depth, organic matter, structure and fertility) (Briske *et al.* 2006, Lopez *et al.* 2011), which underpin key species recruitment and community assembly processes (Prober *et al.* 2002b, Henkin *et al.* 2007, Lopez *et al.* 2011).

Alternative stable states in state-and-transition models (STMs) are defined by community composition, structure and ecological function, within an ecological system or landscape unit (Westoby *et al.* 1989, Stringham *et al.* 2003, Briske *et al.* 2008). A stable state can encompass a number of state phases between which the ecosystem may move in response to changes in the historical disturbance regime under which it has evolved and to which it is adapted (Scheffer and Carpenter 2003, Briske *et al.* 2008). This dynamism is inherent in healthy well-functioning ecosystems and falls within the stability regime of the ecosystem as long as rates of fundamental primary processes such as hydrology, energy capture, and nutrient cycling are not significantly altered (Stringham *et al.* 2003). For example, Colloff and Baldwin (2010) describe floodplain and wetland ecosystems in semi-arid environments such as occur in the Murray Darling Basin as a single state, despite significant transitions between wet and dry phases driven by episodic floods and droughts, as the species assemblages occurring in these systems are adapted to both drought and flooding. Alternatively, a similarly dynamic stable state, incorporating state phases within a stability domain, may develop in response to a new set of stabilising feedbacks under novel environmental conditions (Carpenter *et al.* 2001).

Transitions between state phases are, by definition, reversible, whereas transitions between alternative states are effectively irreversible without active management. Such 'critical' transitions involve thresholds, across which one or more primary ecological properties or processes change (Friedel 1991, Groffman *et al.* 2006). A threshold may be defined by significant change in functions that determine and regulate the dynamics of an ecosystem, resulting in severely diminished resilience (Lopez *et al.* 2011) and a shift to alternative ecosystem states with different sets of stabilising feedbacks and different structural and functional characteristics (Bestelmeyer et al. 2009, Lopez *et al.* 2011).

Resilience-based STMs

Briske *et al.* (2008) have recently proposed modifications to the STM framework to incorporate factors relevant to current understandings of ecosystem resilience, such as feedbacks, community phases vulnerable to change, triggers and restoration pathways (listed and defined in Table 7.1) which better describe dynamics within, and changes between, states. This approach aims to provide a unified framework that links ecological theory and processes with management. The focus in such a model is to highlight understanding, and knowledge gaps in the understanding, of threshold mechanisms and potential trajectories in alternative post-threshold states, in recognition of the critical consequences for land management associated with ecosystem state changes on individual ecological sites. This provides the opportunity to identify at-risk community phases, potential environmental triggers and threshold categories as ecological benchmarks to describe the probability/risk of threshold progression and to increase insight into the feedback mechanisms that determine resilience in the preferred state and drive critical transitions across thresholds (Briske *et al.* 2006).

Table 7.1 Resilience-based concepts recommended for incorporation in the state-and-transition modelling framework (after Briske et al. 2008)

Concept	**Definition**	**Reference**
Alternative states	Temporally or spatially separated plant community states (incorporating phase-changes within states), with characteristic composition, structure and function associated with a regime of environmental variability (e.g. fertility, hydrology, management, disturbance), occurring on similar soils within a local area	Holling 1973, Walker *et al.* 1999, Gunderson 2000, Stringham *et al.* 2003
At-risk community phase	Plant community phase that is most vulnerable to exceeding the limits to resilience of the state, and most likely to undergo transition to an alternative state.	Folke *et al.* 2004, Walker *et al.* 2004
Ecological resilience	System capacity to maintain its fundamental structure and function through stabilising feedback mechansims when subject to disturbance or change.	Holling 1973, Walker *et al.* 1999, Gunderson 2000, Chatham *et al.* 2009
Feedback mechanisms	Ecological processes that enhance (i.e. stabilising negative feedbacks) or decrease (i.e. destabilising positive feedbacks) ecosystem resilience.	Peterson *et al.* 1998, Briske *et al.* 2006, 2008
Feedback switch	Point at which system feedbacks shift from being dominated by stabilising negative feedbacks, that enhance ecosystem resilience and maintain a state in a particular stability domain, to being dominated by positive feedbacks that decrease ecosystem resilience and increase the probability of state change.	Suding *et al.* 2004, Grigulis *et al.* 2005, Scheffer *et al.* 2005, Briske et al. 2006, Hagerthy *et al.* 2008
Restoration pathway	Re-establishment of a desirable pre-threshold state requiring active restoration of the stabilising (negative feedback) mechanisms required to maintain that state.	Suding et al. 2004, Young *et al.* 2005, Bestelmeyer 2006, Briske *et al.* 2006, 2008, King and Hobbs 2006
Thresholds	Levels of biotic (e.g. invasive species) and/or abiotic conditions which exceed the limits of ecological resilience and induce changes (often non-linear) in ecosystem structure and/or function, resulting in a shift to alternative states.	Friedel 1991, Scheffer *et al.* 2001, Scheffer and Carpenter 2003, Chapin *et al.* 2006b, Groffman *et al.* 2006, Suding and Hobbs 2009
Transitions	Transitions are vectors of change. They may be either reversible (occurring between phases within a state) or irreversible/'critical' (occurring between alternative states when a threshold has been breached).	Stringham *et al.* 2003, Briske *et al.* 2006
Triggers	Biotic or abiotic variables or events which act independently or in combination to initiate threshold-related processes (feedback switch, regime shift) by contributing to critical loss of ecosystem resilience in an ecosystem state.	Rietkerk and van de Koppel 1997, Scheffer *et al.* 2001, Mayer and Rietkerk 2004, Briske *et al*. 2006, 2008

7.1.2 Conceptual modelling of floodplain/riparian ecosystems

While there have been many STMs developed for rangeland situations to represent and predict ecosystem responses to grazing disturbance, this approach is rarely applied to riparian ecosystems (Stringham *et al.* 2001, Wondzell *et al.* 2006), despite widespread recognition that these systems are often significantly impacted by altered hydrological regimes and within-patch management regimes (Chapter 1). Baker and Walford (1995) tested the 'state and transition' concept in riparian vegetation on a river reach in southwestern Colorado. They describe a mosaic of patches of different ages since flooding, but found no consistent pattern of post-flood succession in trends in species richness, mean percent cover, and species composition, suggesting differing successional trajectories (to alternative stable states) in response to exceptional flooding events which significantly altered the physical environment. Colloff and Baldwin (2010) used an STM approach to conceptualise ecosystem resilience in the semi-arid floodplain and wetland ecosystems of the Murray-Darling Basin. The model for these systems is based on a single state with transitions between wet and dry phases driven by episodic floods and droughts. Colloff and Baldwin (2010) conclude that floodplains and wetlands in semi-arid environments are subject to strong, periodic abiotic disturbances and that ecosystem functions and biogeochemical processes in such systems are driven by spatio-temporal variability and assemblages of species adapted to both drought and flooding.

Colloff and Baldwin (2010) suggest that the primary mechanism through which resilience is lost, and the potential for a critical transition to an alternative state increased, in semi-arid floodplain and wetland ecosystems is extreme drying outside the range historically experienced in these systems (e.g. due to climatic change and/or over-allocation of water resources). This concurs with the findings of Stringham *et al.* (2001) who developed an STM for riparian ecosystems in a semi-arid floodplain production landscape, subject to groundwater extraction for pasture irrigation purposes, in eastern Oregon, USA. Four distinct plant community states were identified, with critical transitions driven by differences in soil moisture content or depth to groundwater during the growing season (Stringham *et al.* 2001). The authors conclude that models of vegetation dynamics based on concepts of non-equilibrium ecology are appropriate tools for conceptualising and predicting change in the riparian ecosystems. They also suggest that vegetation change in response to soil water and groundwater gradients in these communities is likely to be step-wise, rather than linear, with community stability or resilience to change maintained up to a critical threshold, but sudden and potentially irreversible change once this threshold is crossed (Stringham *et al.* 2001).

7.1.3 This study

This research sought to identify key patterns and drivers of ecosystem condition and function in remnant floodplain riparian woodlands associated with agricultural production landscapes of the northern Murray-Darling Basin (MDB), eastern Australia, to better understand the role of altered disturbance in these systems. It investigated links between landscape pattern, hydrological flows, patch management, and the composition and condition of riparian woodlands in an intensively developed section of the Upper Condamine floodplain, southern Queensland.

Eucalyptus camaldulensis/E. tereticornis woodlands on the Upper Condamine floodplain are significantly reduced in extent (Chapter 2), and, as confirmed in this study, generally in poor condition. This research indicates significant response in floristic composition, community structure and functional diversity, and potentially resilience (i.e. vulnerability) to future disturbance, to gradients in land use intensity, resource availability (including shallow groundwater) and the abundance of the dominant invasive species *Phyla canescens* (lippia) in these riparian woodland remnants. High levels of *P. canescens* are evident across all study sites (Chapter 3), associated with land use intensity (in this case, the proportion of irrigation cropping and grazing land uses; Chapter 5), and facilitated, under certain circumstances, by a close association with the presence of trees (Chapter 6). Moderate to severe dieback is prevalent in mature *E. camaldulensis/E. tereticornis* trees (Chapter 4), indicating significant environmental stress within this landscape associated with land use intensity, chronic groundwater decline, and within-patch grazing (Chapter 5). This is accompanied by limited recruitment in this dominant canopy species complex, but increasing abundance of the subdominant canopy species *Acacia stenophylla*, particularly where eucalypt decline/dieback severity is greatest and tree density is lowest (Chapter 5). Significant changes in floristic composition and functional group transition ratios were also apparent in response to gradients in groundwater decline, tree condition and lippia cover in this landscape (Chapter 5).

This chapter synthesises these findings into a conceptual resilience-based STM (Briske *et al.* 2008) or response model for riparian woodland communities on the Upper Condamine floodplain. The proposed model identifies key observed and potential ecological states and critical transitions between these, based on evidence of association derived from this study and from a review of the relevant literature.

7.2 Methods

Key findings from this research were organised into a state and transition model framework comprising key states and transitions between these in response to major changes apparent in the Upper Condamine floodplain landscape. Modifications to the base STM framework (comprising alternative states and transitions) which better describe dynamics within, and changes between, states in a resilience-based STM, proposed by Briske *et al.* (2008), were incorporated. This approach includes factors relevant to current understanding of ecosystem resilience (i.e. feedbacks, community phases vulnerable to change, triggers and restoration pathways etc., as defined in Table 7.1).

7.3 Results and discussion

7.3.1 A resilience-based STM for riparian woodlands on the Upper Condamine floodplain

Components of a proposed state and transition model (STM) for riparian woodlands on the Upper Condamine floodplain are outlined in Table 7.2. This table, based on the resilience-based STM components suggested by Briske *et al.* (2008), lists:

(i) proposed indicators for each of the proposed ecosystem states (S1-S4);

(ii) negative or stabilising feedbacks potentially operating to maintain each state;

(iii) the at-risk community phase which is most likely to undergo transition to the alternative state (S_{x+1});

(iv) possible trigger events or tipping points which result in the proposed feedback switch (negative to positive); and

(v) subsequent critical transitions across thresholds (T1-T3) to alternative states.

Key states and critical transitions are presented graphically in Figure 7.1.

Table 7.2 Components of a proposed resilience-based state and transition model (STM) for riparian woodlands on the Upper Condamine floodplain (after Briske et al. 2008). Descriptions of alternative states (S1-S4) include indicators of vegetation states and within-state phases (including the at-risk community phase), feedbacks and triggers; proposed transitions (T1-T3) describe possible thresholds.

	Factor	Description
S1	Indicators	Dominant canopy of *Eucalyptus camaldulensis/E. tereticornis,* with some evidence of dieback in response to grazing and/or drought intensity (Davidson *et al.* 2007), pulse recruitment in response to flood events, and a range of size/age classes where grazing is limited (Dorrough and Moxham 2005, George *et al.* 2005); with or without an *Acacia* sp. sub-canopy; diverse perennial groundcover species composition (C3 and C4 habitat generalists and species adapted to grazing, drought and flooding) (Mcintyre *et al.* 1999b, Colloff and Baldwin 2010); inter-tussock patches small and disconnected and occupied periodically by short-lived native species (Stromberg *et al.* 2009)
	Stabilising feedbacks	Perennial groundcover minimises soil, nutrient and water movement from high intensity storms and flooding, and enhances infiltration (Yates *et al.* 2000); deep-rooted canopy species with access to shallow groundwater maintain condition and facilitate persistence of groundcover species during drought periods (Elmore *et al.* 2003, 2006a); persistent propagule/seedbanks facilitate recovery with flooding and/or return to normal conditions (Capon 2007).
	At risk community phase	Native and perennial groundcover low and patchy, large interconnected patches of bare ground periodically occupied by short-lived and/or grazing-resistant species (Yates *et al.* 2000, McIvor *et al.* 2005, Truscott *et al.* 2008)
	Trigger	Land use practices, including grazing within remnants +/- cropping in the surrounding matrix, +/- drought reduce resilience and increase susceptibility to invasive species (Truscott *et al.* 2008, Price *et al.* 2011, Chapter 5)
T1	Threshold	Introduction and flood dispersal of lippia in the landscape (Stokes *et al.* 2007, 2008)
S2	Indicators	Dominant canopy of *Eucalyptus camaldulensis/E. tereticornis,* with some evidence of dieback in response to grazing and/or drought intensity (Chapters 4 and 5), pulse recruitment, in response to flood events, and a range of size/age classes where grazing is limited (as above); with or without an *Acacia* sp. sub-canopy; diverse perennial groundcover species composition (habitat generalists and species adapted to grazing, drought and flooding) (Chapters 3 and 5). Bare patches occupied by lippia after flooding (MacDonald 2008, Price *et al.* 2011); lippia consolidation (phalanx growth habit) where groundcover is reduced due to grazing and/or flooding and soil moisture is retained (Price *et al.* 2008, 2011)
	Stabilising feedbacks	Healthy (functional) deep-rooted canopy species access and redistribute subsoil moisture and/or groundwater through well-functioning surface roots, maintaining tree health and facilitating persistence (limiting loss) of groundcover species, including lippia, during drought periods (Chapter 5)
	At risk community phase	Lippia dominant under tree canopies (Chapters 5 and 6) and potentially competitive with trees for scarce soil moisture resources during drought (e.g. Ludwig *et al.* 2004a); grazing livestock contribute to soil compaction, reduced moisture infiltration and constrain eucalypt surface root condition and function (Yates *et al.* 2000); reduced access to surface soil moisture contributes to drought stress responses in trees (tip death, cavitation, branch sacrifice, reduced productivity, increased susceptibility to infection etc (Alder *et al.* 1996, Rice *et al.* 2004)
	Trigger	Drought and associated soil moisture stress, exacerbated by present of grazing livestock and/or increased competition (especially from lippia) for limited soil moisture resources (Chapters 5 and 6)
T2	Threshold	Water management (altered hydrological regime, water diversion, extraction) which contributes to groundwater decline in shallow alluvial aquifers (CSIRO 2008, Chapter 2) below levels (e.g. 15 m) which support tree health (Chapter 5) and survival during periods of critical soil moisture deficit (Horner *et al.* 2009).
S3	Indicators	Mature *Eucalyptus camaldulensis/E. tereticornis* sparsely distributed and in poor

	Factor	Description
		health (moderate-severe dieback), with significant numbers of stags and little successful recruitment (restricted age distribution) (Chapters 4 and 5); increasing levels of dieback in response to hydrological stress +/- grazing (Chapters 4 and 5). Increasing prevalence of *Acacia* spp. where grazing is excluded (Chapter 5). Groundcover floristics dominated by lippia (Chapter 3); non-lippia vegetation comprising resistant perennial groundcover species (species adapted to grazing, drought and/or flooding) (Mcintyre *et al.* 1999b, Colloff and Baldwin 2010, Chapter 6). Lippia persistent in drought refugia under trees (Chapter 6)
	Stabilising feedbacks	Some recovery of tree condition and groundcover composition with good rainfall and/or flooding which disperses propagules and replenishes surface and subsoil moisture reserves (Amlin and Rood 2003, Yurkonis and Meiners 2006)
	At risk community phase	Tree condition fails to respond to improved soil moisture conditions, evident as ongoing incremental loss/mortality of mature eucalypts and recruitment failure despite adequate rainfall and/or flooding (Cox *et al.* 2005, Croft *et al.* 2007, Jensen *et al.* 2007). Poor tree health and lippia infestation are also contributing factors in decisions to clear smaller unmapped remnants not covered by tree clearing legislation under the *Vegetation Management Act 1999*, contributing significantly to reduced extent and increasing fragmentation of this vegetation type (pers. obs.).
	Trigger	Biotic failure of canopy tree species (loss of root function, hydraulic failure, increased susceptibility to infection/infestation, reproductive failure) +/- exacerbated by drought (Croft *et al.* 2007)
T3	Threshold	Low patch-scale cover of riparian eucalypts, poor propagule dispersal and recruitment resulting in a demographic failure in the *Eucalyptus camaldulensis/E. tereticornis* metapopulation (e.g. Aldrich and Hamrick 1998)
S4	Indicators	S4a: dominant canopy of *Acacia stenophylla* where flooding occurs and/or soil conditions are suitable (CSIRO 2004, Doody *et al.* 2009) and grazing is restricted (Chapter 5); groundcover of flood- and drought-resistant species (Chapter 5) and/or nitrogen-dependent (nitrophilic) species (Prober *et al.* 2002b, 2005), including lippia (Clech-Goods 2010); and/or S4b: limited woody species canopy where soil or moisture constraints/grazing occur (potentially another threshold, T4) (Scholes and Archer 1997, Mills *et al.* 2006); diverse perennial graminoid groundcover species composition (habitat generalists and species adapted to drought and flooding) under sustainable grazing/where grazing is excluded (i.e. conversion to floodplain grassland); grazing-resistant grassland/herbfield where overgrazing occurs (McIvor *et al.* 2005), with lippia potentially dominant under adequate soil moisture conditions (Price *et al.* 2010a, Berney *et al.* 2010).
	Stabilising feedbacks	Perennial groundcover minimises soil, nutrient and water movement with high intensity rainfall and flooding, and enhances infiltration (Yates *et al.* 2000); persistent propagule-/seed-banks facilitate recovery with flooding and/or return to normal conditions (Capon 2007); limited availability and/or dispersal of *Eucalyptus camaldulensis/E. tereticornis* seed material within the landscape (Dorrough and Moxham 2005, George *et al.* 2005, Jensen *et al.* 2007, 2008a,b). Where *Acacia* species dominate, nitrification and nitrogen cycling maintain high levels of nitrophilic species (e.g. Prober *et al.* 2002b), potentially including lippia (Clech-Goods 2010).

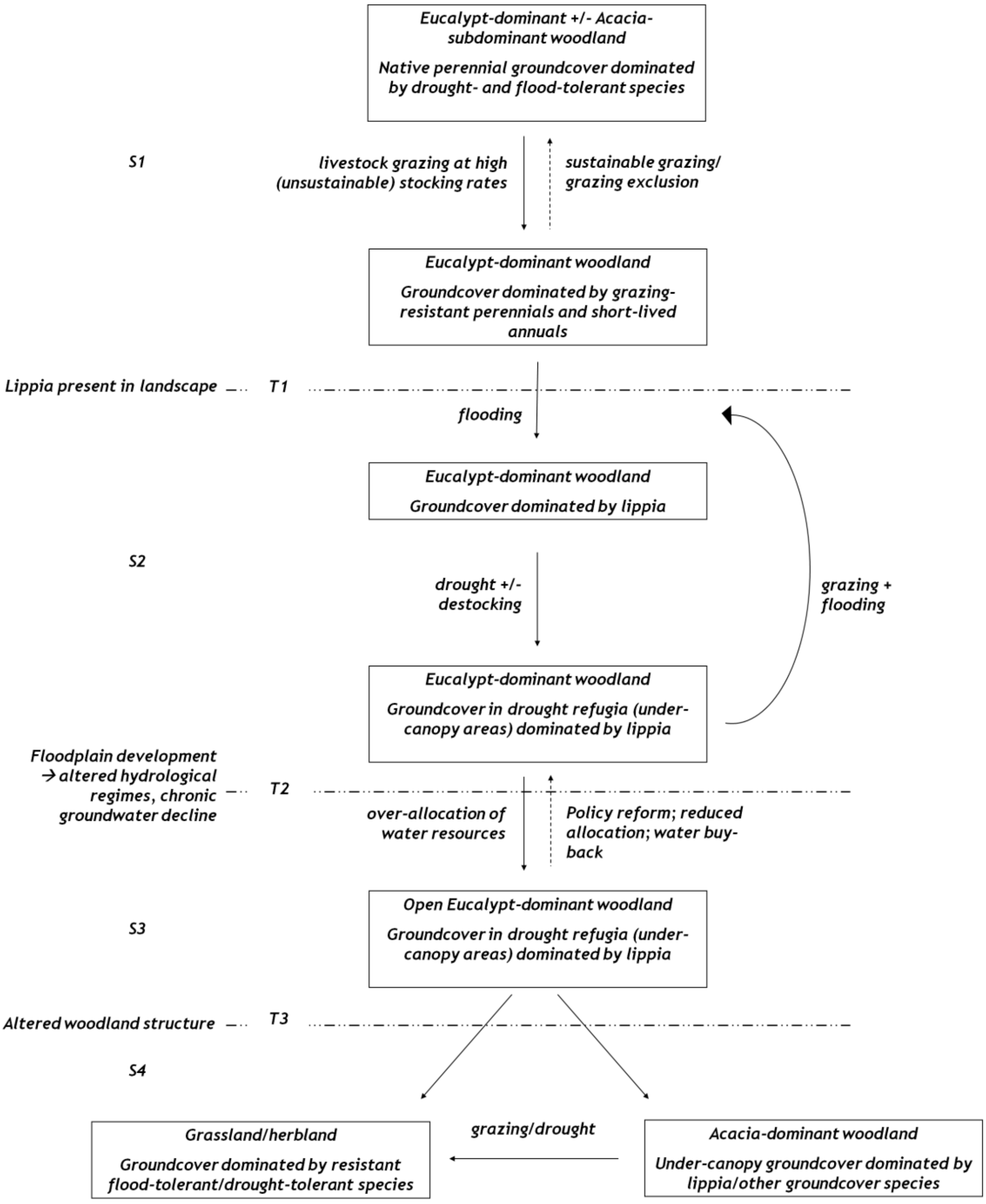


Figure 7.1 A conceptual state and transition model for Upper Condamine floodplain riparian woodland. Only key phase changes within states are indicated. Transitions are indicated by solid arrows; restoration pathways are indicated by dashed arrows; and critical thresholds (biotic, management) are shown as broken lines. Detailed descriptions of states and feedbacks are provided in Table 7.2.

The proposed conceptual resilience-based state and transition model for riparian woodland ecosystems of the Upper Condamine floodplain (Table 7.2, Figure 7.1) comprises four key alternative ecological states (S1-S4) separated by three critical transitions and potential thresholds (T1-T3) between these. These include a pre-lippia landscape (S1), with riparian grassy eucalypt woodland composition exhibiting reversible transitions (not shown in Figure 7.1, but described in Table 7.2) between within-state phases in response to episodic flood and drought events (Colloff and Baldwin 2010). Livestock grazing, a novel disturbance in these ecosystems, is likely to have driven transitions to alternative states with significantly altered floristic composition and community structure, as has been found in other situations (e.g. Spooner and Allcock 2006, McIntyre and Lavorel 2007); however, this was not able to be tested in this study, which was conducted in a post-invasion lippia-dominated landscape (S2).

Transition to a lippia-invaded landscape

The critical transition (T1) between these two alternative states represents an irreversible change associated with the introduction and spread of lippia within the Upper Condamine floodplain landscape, creating a novel ecosystem type (*sensu* Hobbs *et al.* 2006, 2009) in which lippia plays a dominant ecological role, facilitated by flooding, grazing, the presence of scattered eucalypts and the intensification of land use (Chapters 5 and 6). Reversal of this transition is highly unlikely, given lippia's capacity to form a persistent soil seedbank (Macdonald 2008) and evidence of its potential for rapid micro-evolution and ongoing adaptation to future disturbances such as climate change (Xu *et al.* 2010a).

Within lippia-invaded floodplain riparian woodlands (S2), lippia is a dominant and functionally important species influencing the composition, structure and function of these woodlands (Chapter 5); however, it is also responsive to a range of disturbance regimes and to the condition (density, height) of non-lippia groundcover vegetation (Chapter 6). Close association between the presence of trees and lippia is evident, with greater lippia cover and reproductive effort in close proximity to trees. This 'halo effect' is in part linked to reduced cover of other (non-lippia) groundcover species close to trees and consequent higher light availability at ground level, but may also be influenced by the concentration of resources (soil nutrients, soil moisture) and altered soil condition associated with the presence of trees in this landscape. Facilitation by trees may provide a critical refuge for this mesic C3 species, enhancing its persistence in this landscape, particularly during periods of severe drought (Chapter 6). Flooding, and a return to ‘normal’ rainfall conditions, in combination with grazing is likely to see lippia abundance increase across the landscape (Price *et al.* 2008, 2010a, Berney *et al.* 2010), with consequent shifts in the floristic composition and structure of these communities (Chapters 5 and 6). Thus phase changes and reversible transitions within S2 are likely to occur in response to climatic conditions (drought, rainfall, flooding), particularly where these occur in combination with levels of grazing which reduce the cover density and height of non-lippia vegetation (Taylor and Ganf 2005, Price *et al.* 2008, 2011, Chapter 6). Critical transitions to alternative states are possible in response to high levels of grazing in combination with suitable soil moisture conditions, but increasing lippia abundance under these conditions generally leads to destocking (Lucy *et al.* 1995) and subsequent native vegetation recovery over time (e.g. QMDC 2005) with ecosystem responses buffered by persistent soil seedbanks and flood dispersal of species propagules from upslope sources. Loss of persistent soil seedbanks due to reproductive failure or extreme drought or flooding, in combination with loss of upstream remnants or flood dispersal limitation due to floodplain flow diversion structures may limit recruitment in these communities (Chapter 5), but this requires further investigation.

Lippia may also exacerbate drought stress in riparian eucalypts, as suggested in Chapter 6. However, chronic decline (increasing dieback severity) in the dominant canopy species in these woodlands, *Eucalyptus camaldulensis/E. tereticornis*, appears to be driven by groundwater decline (Chapters 4 and 5). *E. camaldulensis* is a deep-rooted phreatic species (Thorburn *et al.* 1993, 1994, Mensforth *et al.* 1994) which is increasingly dependent on accessible groundwater resources during periods of surface soil moisture deficit (Thorburn *et al.* 1993, Doody *et al.* 2009). It is capable of accessing subsoil moisture and groundwater to depths of approximately 15 m (Mensforth *et al.* 1994, Horner *et al.* 2009), and passively redistributing this water from deep sinker roots to shallow surface roots and surface soils (Burgess *et al.* 1998). This process (hydraulic lift) has been shown elsewhere to contribute to the maintenance of the surface root systems of trees during periods of limited precipitation and low soil moisture (Burgess *et al.* 1998, Scholz *et al.* 2002), and to enhance the abundance and diversity of neighbouring groundcover (Ludwig *et al.* 2004b) and shrub (Zou *et al.* 2005) species. In this study, groundwater level is a strong predictor of groundcover composition; this is potentially mediated through the hydraulic function of mature eucalypts in the study landscape (Chapter 5), indicating that trees may well be critical (keystone) elements contributing to functional response and resilience in these communities.

Transition to groundwater-independent riparian woodlands

A second critical transition (T2), from a riparian landscape buffered by groundwater connectivity (S2) to one disconnected from groundwater (S3), is effectively a socio-ecological threshold (Anderies *et al.* 2006, Chapin *et al.* 2006b, Folke 2006) associated with the development of irrigated agriculture on the Upper Condamine floodplain and currently supported by high levels of water resource use in this region (Chapter 2). Chronic groundwater decline/falling groundwater levels are evident in bore hydrographs since the commencement of irrigated agriculture in the 1960s, and, despite significant flood events in that period, there is no evidence of recovery. This has resulted in groundwater depths which now, in parts of the riparian landscape, potentially exceed levels accessible to deep-rooted phreatic species such as *Eucalyptus camaldulensis/E. tereticornis*, potentially leaving these more susceptible to drought stress and contributing to dieback responses (Chapter 5) and increased mortality (Horner *et al.* 2009).

Increasing groundwater depth and poorer tree health in this study were associated with changes in groundcover composition and functional diversity under drought conditions at the time of sampling. In semi-arid ecosystems elsewhere, access to shallow groundwater provides a stabilising buffer to drought and is an important factor in the composition, structure, function and resilience of these ecosystems (e.g. Elmore *et al.* 2006a). Loss of deep-rooted woody vegetation due to groundwater decline may contribute not only to significant change in floristic composition in associated herbaceous vegetation, but also to increasing sensitivity and vulnerability to climatic events (e.g. Elmore *et al.* 2006a).

Transition to alternative riparian ecosystem types

Increased drought susceptibility and declining condition of mature riparian eucalypts under drought conditions, in combination with poor recruitment in these species (Chapter 5), may be indicative of eventual population failure (Rice *et al.* 2004, George *et al.* 2005, Jensen *et al.* 2008a). This represents a third critical transition (T3) from an ecosystem state where these canopy eucalypts, despite declining condition and function, still dominate (S3) and an alternative state (S4) in which they are effectively absent due to population failure in these ecosystems. Disconnection from groundwater in similarly adapted phreatic riparian tree species is reported to cause significant canopy dieback and physiological failure (embolism, cavitation), contributing to increased mortality within local populations (e.g. Cooper *et al.* 2003b, Froend and Drake 2006) and shifts in dominance within ecosystems (e.g. Shafroth *et al.* 2000, Stromberg *et al.* 2007b). Although not tested in this system, accessible groundwater is likely to be the critical factor delimiting the extent of floodplain woodlands and grasslands on the floodplain. Bren (1992) reports invasion of a floodplain grassland ecosystem by *Eucalyptus camaldulensis* in response to rising groundwater levels on the Moira grass *Pseudoraphis spinescens*-dominated War Plains in the southern Murray Darling Basin, indicating that the converse (i.e. decline in *E. camaldulensis*) may also be true where groundwater levels are falling. On the Upper Condamine floodplain, it is likely that the declining extent of *E. camaldulensis/E. tereticornis* woodlands due to groundwater decline would result in replacement of current riparian woodland communities.

The alternative non-eucalypt riparian ecosystem state (S4) is likely to comprise community phases of low woodlands or shrublands dominated by *Acacia* species (e.g. *A. stenophylla*), floodplain grasslands (where lippia cover is low) or herblands dominated by lippia (Table 7.2, Figure 7.1). This alternative state may not be realised for considerable time after a threshold for eucalypt persistence has been passed in this landscape due to significant lags in responses, as well as the capacity for short-term adaptive recovery, in long-lived species such as *Eucalyptus camaldulensis/E. tereticornis*. However, chronic decline in this species complex is already apparent in this landscape in terms of the health of mature trees (Chapter 4). Coupled with poor recruitment and survival of recruits, it is likely that this decline will persist, and potentially increase, over time with declining tree health and increased frequency and intensity of drought conditions associated with predicted climate change (Dorrough and Moxham 2005, George *et al.* 2005, Jensen *et al.* 2007, 2008a,b). A demographic study of canopy species in riparian woodlands of the Upper Condamine has not been conducted, but would provide valuable evidence of population trends.

7.3.2 Significance and limitations

The synthesis of results from this current research, in combination with evidence from previous studies in similar ecosystems elsewhere, into a resilience-based state and transition model provides insight into the potential for retention of riparian *Eucalyptus camaldulensis/E. tereticornis* woodland ecosystems on the Upper Condamine floodplain, a highly modified production landscape. It also identifies critical gaps in our current knowledge and understanding of these systems, and provides direction for future research to fill these.

Briske *et al.* (2008) argue that the organisation of knowledge and understanding of an ecological system into a resilience-based STM is a means of focusing attention on management and policies which promote within-state resilience and reduce the potential for state transitions across critical thresholds (i.e. effectively, the limits of state resilience). However, this presumes an accurate knowledge of the mechanisms involved and the identification of valid indicators of change, as well as the capacity to influence the key drivers of change. On the Upper Condamine floodplain, it appears that thresholds have been crossed; however, critical transitions between alternative states may not yet be fully realised due to lag times in ecosystem response (Chapin *et al.* 1993, Scott *et al.* 1999). This is particularly the case with T2, the groundwater depth threshold in this model. Significant responses in long-lived adaptive species such as *Eucalyptus camaldulensis/E. tereticornis* may not be evident for some time after such a threshold is crossed, due to the species’ capacity to access water from a variety of sources and adaptive responses such as canopy thinning to reduce evaporative demand (Chaves *et al*. 2003, Doody and Overton 2009) and epicormic regrowth following stress (Landsberg and Wylie 1983, 1988, Marsh and Adams 1995). It is likely that severe drought conditions contribute to a critical rate of change in trees already responding to chronic groundwater decline. Management intervention (if feasible) in these situations is likely to be inadequate in a system in which there is only limited capacity to redress the situation. For example, the volume of stored water in the Upper Condamine river system is relatively small and the provision of environmental flows is unlikely to contribute significantly to groundwater rise in a system in which surface and ground waters are effectively disconnected along much of this section of the river (CSIRO 2008).

Conversely, better definition of potential thresholds may contribute to the identification of sites at which groundwater is still within the accessible range, and may form the basis for strategic management of these sites and of groundwater levels in their vicinity. While new developments such as the emerging coal seam gas industry in southern Queensland are fraught with potential environmental problems (Moran and Vink 2010), the quantity of water likely to be extracted and available for re-use may represent an opportunity, where appropriate water quality can be assured, to supplement groundwater at high priority sites. Similarly, in-stream weirs appear to ameliorate the impacts of groundwater decline on tree condition in areas immediately downstream; in-stream barriers (weirs and large woody debris) which act to slow flow and retain water within the system may contribute to locally enhanced groundwater conditions to support better tree health (Chapter 4 and 5). Both options appear worthy of further investigation to ascertain their feasibility and potential contribution to improved groundwater connectivity.

This STM captures only the primary drivers of change in these woodlands. To accurately incorporate the range of disturbances which impact on riparian woodland systems in the Upper Condamine landscape (as indicated in Chapter 5) would lead to a potentially complex array of states, phases and transitions for which there is currently little empirical evidence. However, it does highlight critical transitions suggested by this research, and point to the value of the state and transition modelling framework as a tool for conceptualising ecosystem dynamics in such a highly disturbed system. It also highlights the need to better understand the mechanisms associated with vegetation change in this landscape, in particular the role of key dominant species in driving changes in floristic composition and community structure.

Further development of this model is also required in order to quantify the probability of change (Bellamy and Brown 1994, Briske *et al.* 2006, Rumpff *et al.* 2011), particularly where this is associated with delayed response. Such a quantitative predictive model would also incorporate probabilities associated with the potential for reversal of critical transitions and restoration of preferred ecosystem states (Young *et al.* 2005, Briske *et al.* 2006), and would provide valuable support to sustainable resource management in this landscape.

While developed for riparian woodland ecosystems on the Upper Condamine floodplain, this STM may also be applicable in similar ephemeral river systems and multi-use landscapes in the northern Murray Darling Basin, particularly where there is evidence of groundwater decline. This might include other irrigated cropping regions, but could also potentially apply where the emerging coal seam gas industry is predicted to place significant pressure on groundwater systems (Moran and Vink 2010). Accurate monitoring of groundwater levels in shallow aquifers supporting water-dependent vegetation, and management to reduce the risk of groundwater decline below levels accessible to phreatic species, may be necessary to avoid risk associated with loss of resilience in these systems (Eamus *et al.* 2006) and transition to less-functional ecosystem states.

7.4 Conclusions

The resilience-based state and transition model developed in this chapter provides insight into the potential for retention of riparian *Eucalyptus camaldulensis/E. tereticornis* woodland ecosystems on the highly modified Upper Condamine floodplain. Significant transitions identified include the historical shift from a pre-invasion lippia-free landscape to one in which lippia is a dominant component of native ecosystems on the floodplain, particularly in locations where flooding and grazing have occurred over time. A second critical transition, driven by chronic groundwater decline associated with the development of irrigated agriculture, is currently being realised in the decline of the dominant phreatic canopy species; this is likely to have been exacerbated by drought conditions, indicating a loss of resilience within these communities. The important functional role played by this species within these woodlands is indicative of a future critical transition from a savanna woodland landscape to one in which trees play a limited functional role. Likely outcomes of this transition are *Acacia stenophylla*-dominant shrubland and floodplain grassland or lippia-dominant herbland ecosystems; further research is required in order to determine the value of these systems in terms of ecosystem service provision.

The potential to redress chronic groundwater decline in this system is limited under current water resource allocation arrangements. However, there is an opportunity to identify parts of the landscape in which groundwater levels remain accessible to *Eucalyptus camaldulensis/E. tereticornis*. This study suggests that these sites should be prioritised in terms of management to maintain woodland function. While further research would be required to define strategies to achieve this, it is apparent that this should include management to stabilise, and possibly supplement, groundwater levels.

Chapter 8 General discussion and conclusions

8.1 Introduction and summary

Remnant ecosystems in agricultural landscapes are relatively poorly understood in terms of their diversity, function and dynamics (resilience) under altered disturbance regimes; yet these ecosystems can contribute significantly to our understanding of how ecological systems respond to change. Such knowledge is vital to our understanding of how major disturbances such as climate change may play out, and how management may most effectively respond to retain biodiversity (ecological diversity and function) and ecosystem services in these important landscapes.

This thesis has reported research results from studies investigating patterns in the composition, structure and condition of *Eucalyptus camaldulensis/E. tereticornis* riparian woodlands on the highly modified Upper Condamine floodplain, southern Queensland. It has contributed new understanding of responses in riparian woodland ecosystems to natural and anthropogenic disturbance on the Upper Condamine floodplain, and also contributes to a more general understanding of the dynamics of ecosystem remnants in highly modified landscapes. While sampling at one point in time, in this case during significant drought, means that the full range of ecological response in these communities was not captured, this study provides an insight into the resilience and resistance to extreme drought of these riparian woodland communities; this may not have been possible if sampling had occurred under more benign conditions. The research was also essentially correlative and exploratory in nature, hence relationships between environmental and response variables cannot be interpreted as indicative of cause and effect without further investigation. In addition, the highly confounded nature of some drivers (Chapters 3, 4 and 5) means that the interpretations presented in this thesis are not exclusive of alternative explanation. However, despite these limitations, this study provides clear indication of significant change in these communities, which has been interpreted in the context of previous research findings and known ecological mechanisms.

Chapters 3 and 4 tested a number of potential ecological hypotheses which are supported in other riparian and riverine systems. These included that patterns in floristic composition, functional diversity and dominant canopy tree species condition are related to differences in in-stream flow or longitudinal connectivity, lateral connectivity across the floodplain (in terms of both overbank flooding and overland flow), and within-remnant land use (i.e. grazed or ungrazed). Key findings of these studies were that significantly lower floristic and functional diversity and poorer tree condition were potentially explained by reduced hydrological variability, concurring with studies elsewhere (e.g. Ward and Stanford 1995b, Stromberg *et al.* 2007a); however, this was confounded by evidence of greater land and water use intensity in these sections of this landscape. Significant interaction between longitudinal connectivity and land use, and, in some cases, lateral connectivity and land use, indicated that a complexity of drivers influence ecosystem patterns in this modified production landscape.

These studies also confirmed that floodplain riparian *Eucalyptus camaldulensis/E. tereticornis* woodlands on the Upper Condamine are in poor condition, exhibiting severe dieback and mortality in dominant canopy eucalypts, as well as significant levels of invasion by the alien clonal groundcover species *Phyla canescens* (lippia), as have been previously reported (Phillips and Moller 1995, McCosker 1996, Voller 1998).

Chapter 5 investigated woodland response to a range of hydrological, land use and land cover variables at a range of scales including within-remnant (patch-scale), peri-remnant (adjacent landscape scale) and multi-remnant (local landscape scales). The majority of response variables (including floristic composition, functional group richness and abundance transitions, and canopy tree attributes and condition) were best explained by a combination of hydrological and land use/land cover environmental variables operating at a range of spatial scales. Key predictors of riparian woodland response in this study were land and water use intensity, including grazing at the within-remnant patch scale (within 500 m), land use intensity and land cover type in the adjacent landscape upslope of sites (within 2000 m), and the density of groundwater bores and extent of irrigated cropping in the ‘local’ landscape (within 5 km) surrounding sites. However, the primary abiotic driver of ecosystem response identified in this study was groundwater decline, with lower diversity and more severe dieback associated with increasing depth to groundwater, suggesting an over-arching reliance on shallow groundwater resources for maintenance of ecosystem resilience. This concurs with findings from similar semi-arid dryland river systems elsewhere, particularly during extended drought when access to groundwater provides a critical buffer to low soil moisture availability (e.g. Amlin and Rood 2003, Elmore *et al.* 2003, 2006); however, this has not previously been reported for systems in the Murray-Darling Basin (MDB) and is counter to current understanding of riparian ecosystem response to water resource development in this river system. In the southern MDB, riparian ecosystem decline is generally driven by rising groundwater levels and associated salinisation. However, interrogation of the records for groundwater monitoring bores in the Upper Condamine confirmed chronic groundwater decline in this landscape over the 50 years of irrigated cropping, with limited recovery in response to wetter periods or extensive flooding (Chapter 2); this is in direct contrast to the prevailing conditions along the River Murray (CSIRO 2008).

Lippia abundance and dieback severity were also found to be important biotic drivers of ecosystem condition in these communities, and key predictors of floristic composition and functional group richness and abundance transitions. Poor tree condition was interpreted as loss of function in terms of hydraulic redistribution of deep soil moisture which acts to supplement shallow soil moisture levels (Burgess *et al.* 1998, Burgess and Bleby 2006) and support species which are less well adapted to the range of climatic variability experienced in this landscape (Colloff and Baldwin 2010). This may result from declining function in eucalypts associated with poor surface root condition due to the impact of grazing livestock on soil structure (Northup *et al.* 2005), inability to repair damaged surface roots due to carbon depletion associated with drought and declining condition (Snyder and Williams 2007), disconnection between deep roots and declining groundwater levels (Williams *et al.* 2006), or a combination of these factors. Responses to lippia abundance were not readily interpreted in terms of possible mechanisms affecting tree decline from the study reported in Chapter 5. However, strong associations between lippia cover and the density and mortality of mature trees indicated that this relationship might be important in this landscape, and was investigated in Chapter 6.

The study reported in Chapter 6 indicates that scattered trees play a significant role in facilitating the abundance and persistence of lippia in this landscape, and that lippia cover above approximately 20% may have a significant impact on the abundance and diversity of non-lippia species in these grassy woodlands. Lippia growing under the canopy of mature trees exhibited high levels of abundance (cover), a consolidated matting growth form and high reproductive levels compared to areas in canopy gaps. There was a strong association between lippia cover and the availability of light at ground level, related to reduced cover of taller-growing non-lippia species under the dappled shade of scattered eucalypts. Lippia growth beyond the canopy edge was predominantly a loosely trailing exploratory 'guerrilla' form, which other studies have shown is supported through clonal integration (Xu *et al.* 2010b) and provides lippia with a capacity for rapid expansion when soil moisture conditions improve (Price *et al.* 2011). Lippia cover was also significantly correlated with the higher levels of organic carbon, chloride and exchangeable cations apparent under tree canopies; however, the mechanism underpinning the apparent increased competitive advantage of lippia over non-lippia species once its cover reaches the potential threshold level of 20% requires further investigation, as does the potential impact of lippia on tree condition.

Key relationships apparent from these studies were summarised in a conceptual resilience-based state and transition 'riparian woodland response' model (Briske *et al.* 2008, Chapter 7), which identified three potential critical transitions for riparian ecosystem condition and function in this landscape. The first transition was lippia invasion of the Upper Condamine landscape, which effectively transformed the riparian woodland communities into novel ecosystems in which lippia was an increasingly dominant and functional component. The second transition was the development of an irrigated agricultural industry which has driven chronic groundwater decline to levels which are effectively beyond access by deep tree roots, contributing to greater vulnerability in these ecosystems to rainfall variability and soil moisture deficit. Increased dieback severity in trees no longer able to access shallow groundwater during drought periods, in combination with recruitment failure, suggest a reduced density of woodland trees in these ecosystems over time. These are likely to be replaced by the subdominant drought-hardy species *Acacia stenophylla* in parts of the landscape close to the river. In other areas, these woodland ecosysytems may be replaced by the alternative floodplain ecosystem on the soil type, *Dichanthium sericeum* grasslands, or lippia-dominant herblands where grazing and flooding disturbances prevail. This transition may occur slowly due to the adaptive capacity of *Eucalyptus camaldulensis/E. tereticornis*; however, at some point it is likely that a threshold response may become apparent with population failure in *E. camaldulensis/E. tereticornis* due to increased mortality triggered by extended drought or recruitment failure due to lack of seed production and limited dispersal, germination and survival of seedlings with extended drought and/or reduced flooding. Such a transition may contribute to a decline in lippia populations in the region, given the apparent role of trees in the persistence of lippia in this landscape, particularly during adverse climatic conditions (Chapter 6). However, it is also probable that there would be significant changes in the level of ecosystem services (e.g. flood tolerance, streambank stability, aquatic ecosystem condition, koala habitat etc) delivered in such an altered landscape.

8.1.1 Importance of surface flow (longitudinal and lateral) connectivity

In contrast to many other studies (e.g. Lite *et al.* 2005, Renofalt *et al.* 2005a,b), differences in surface flow connectivity, while apparent, were not clearly identified as dominant drivers of ecosystem condition or heterogeneity in this study. This may have been, in part, a result of the prevailing drought conditions and the lack of any major rainfall or flood events in the years preceding sampling, and cannot be interpreted as indicative of low importance to these ecosystems. Evidence of low recruitment in riparian eucalypt species alone suggests that lack of periodic inundation by floodwaters is likely to have significant long-term impacts on the population dynamics of these important canopy species (George *et al.* 2005, Jensen *et al.* 2008a), and subsequent impacts on the long-term function and resilience of these communities (Chapter 7). However, this is also potentially linked to the strong influence of additional disturbances associated with land use intensity in this highly modified landscape. Evidence of reduced floristic and functional diversity and poorer tree condition in the Middle river section (Chapters 3 and 4) coincided with limited streamflow dynamics in the years preceding sampling; however, they were also associated with greater levels of land use change and higher land and water use intensity in this section of the study area (Chapter 2). Relatively better tree condition on the Lower river section suggests the potential for in-stream weirs to influence local shallow groundwater flows, as suggested by others studies (e.g. Lane and Zinn 1980); however, this requires further investigation.

This study does indicate that overland flows which connect riparian remnants with the broader upslope landscape are likely to be important factors influencing the richness and diversity of species in riparian remnants. Evidence of significant functional group response to land use type and intensity and the presence of off-stream water storage infrastructure in the adjacent area upslope of riparian woodlands indicates that diversion of overland flow might significantly influence the dynamics and resilience of these ecosystems remnants. This effect has not been empirically demonstrated, and requires further investigation to determine whether this response is due to constraints on the dispersal of species propagules (e.g. Malanson and Armstrong 1996, Van Dorp *et al.* 1997) or changes in sedimentation, water inflows and/or water infiltration rates (Porter 2002, Bramley *et al.* 2003, Beauchamp and Stromberg 2008).

8.1.2 Importance of vertical connectivity

Vertical connectivity between surface and groundwater systems is increasingly acknowledged as an important component of riverine systems in Australia, with baseflow from shallow alluvial aquifers providing a critical buffer to in-stream flows during low rainfall runoff periods (e.g. Boulton and Hancock 2006, Evans and Neal 2006). However, the importance of shallow groundwater systems to riparian vegetation condition has received little attention, despite evidence from other parts of the world that this can be a critical factor, particularly in riparian ecosystems associated with semi-arid dryland river systems (e.g. Stromberg *et al.* 1996, Brunke *et al.* 2003, Elmore *et al.* 2003, 2006a). In contrast, the focus in Australia has been on the degradation of riparian systems in response to rising groundwater and salinity levels in regions, such as the southern MDB, where widespread clearing of deep-rooted vegetation across catchments has significantly altered landscape hydrology (e.g. Jolly *et al.* 1993, Slavich *et al.* 1999, Overton *et al.* 2006) and where water management regimes maintain high in-stream, and, by association, alluvial groundwater levels (Overton *et al.* 2006). Significant impact on riparian systems is reported where altered hydrological regimes contribute to prolonged periods of inundation or where shallow groundwaters carry high salt loads and contribute to raised soil salinity levels (Jolly *et al.* 1996). There are few cases in Australia where groundwater decline is considered detrimental to a native vegetation community.

These include the Gnangara Groundwater Mound in Western Australia, where phreatic *Banskia* species suffer significant impact from groundwater drawdown associated with mining activities in the local area, particularly through seasonal summer drought periods (Zencich *et al.* 2002, Froend and Drake 2006, Canham *et al.* 2009). Horner *et al.* (2009) also report increased mortality in a densely planted maturing *Eucalyptus camaldulensis* plantation where groundwater levels exceeded 12–15 m.

Chronic groundwater decline is apparent in the Condamine Alluvium, the shallow alluvial aquifer associated with the Upper Condamine River. This has likely been driven by high levels of groundwater extraction to support irrigated agriculture over a period of 50 years, resulting in recorded declines of up to 20 m in some monitoring bores (Chapter 2). In this study, groundwater depth was a key predictor of floristic composition, functional diversity and mature tree condition. Other studies have reported the critical importance of vertical connectivity between shallow groundwater resources and ecosystem condition, particularly during periods of soil water deficit (e.g. Amlin and Rood 2003, Elmore *et al.* 2003, 2006a), suggesting that accessible groundwater provides a critical buffer against drought impacts in semi-arid water-dependent riparian systems.

8.1.3 Importance of landscape legacy

Several studies have indicated the critical influence of past land use and disturbance on current composition, structure and function in ecosystems (Lunt and Spooner 2005, Cousins 2009), although this legacy is often not readily taken into account in studies of ecosystem response (Dale *et al.* 2000). Increasing use of geographic information systems to record and interrogate spatially linked datasets provide a rich opportunity for tracking change through time (Elmore *et al.* 2006b). This may be particularly valuable for interpreting change in long-lived adaptive species such as canopy eucalypts, which may exhibit significant time-lags in response to environmental change (Kozlowski and Pallardy 2002, Vesk *et al.* 2008), and would facilitate predictive modeling of future change in these ecosystems (Chapter 7). Such temporal connectivity was not specifically measured in this study, which was effectively a snapshot in time. Despite this, greater dieback severity in dominant canopy eucalypts in response to groundwater depth may be interpreted as indicative of future trends in the composition, function and resilience of these woodlands with continued groundwater extraction and climate change impacts on in-stream flows and groundwater recharge (Scott *et al.* 1999, Horton *et al.* 2001a, Chapter 5). Similarly, functional group transitions to higher relative richness and abundance of floodplain or wetland species, due to loss of generalist/terrestrial species with increasing groundwater depth and dieback severity, indicates reduced ecosystem diversity but potentially increased resistance to change (Colloff and Baldwin 2010, Chapter 5), at least in the short-term.

In addition, persistent soil seedbanks, and propagule dispersal from upstream remnants, are likely to play a critical role in buffering ecosystems against major shifts in species composition in landscapes which are increasingly subject to modification with the intensification of land use and altered frequency, intensity and duration of drought and flooding disturbance events associated with predicted climate change (Capon and Brock 2006, Capon 2007, Stromberg *et al.* 2008). Such persistence through time is also a critical component of the success of alien species, such as lippia *Phyla canescens*, within an invaded landscape. Interactions between the autecology of lippia and flooding and grazing disturbance regimes have promoted its spread and establishment within floodplain landscapes (Macdonald 2008, Macdonald *et al.* 2006, Price *et al.* 2008, 2011); however, persistence of this mesic species through periods of extended soil moisture deficit is perhaps critical to its success in this semi-arid landscape. Previous studies have indicated lippia's ability to form a persistent soil seedbank, with evidence of adaptation to defer germination until conditions are likely to ensure successful establishment (Macdonald 2008, Macdonald *et al.* 2006). This current study indicates that lippia persistence is also facilitated by large trees (and also potentially micro-topographic variations) which provide significant drought refugia for lippia in this landscape, enhancing its survival, abundance and reproductive success through periods of soil moisture deficit and also its potential to respond rapidly to improved soil moisture conditions with return to normal rainfall conditions and flooding (Chapter 6).

8.2 Management and policy implications

Biodiversity investment decisions need to balance the probability of success against perceived value in terms of biodiversity conservation and landscape health outcomes (e.g. protection of threatened species and ecosystems, maintenance of critical ecological processes/ecosystem services) (Chapin *et al.* 2000, Swift *et al.* 2004, Hobbs *et al.* 2006). This implies that we understand the critical drivers of change in modified ecosystems, and that we have the capacity to address these. Improved understanding of how individual systems respond to anthropogenic change is vital to ensure that investment and management are tailored to effectively address specific issues within local contexts, including critical thresholds which might constrain ecosystem recovery and restoration (Hobbs and Harris 2001, e.g. Prober *et al.* 2005).

Determining the relative importance of different environmental drivers of ecosystem condition is a critical challenge to biodiversity conservation in complex highly modified landscapes (Folke *et al.* 2004, Heller and Zavaleta 2009). This is especially the case in socio-ecological systems (Carpenter *et al.* 1999, Kinzig *et al.* 2006), such as multi-use production landscapes (e.g. Shelton *et al.* 2001). Such systems are poorly studied (Kinzig *et al.* 2006), and may be particularly complex and prone to delayed responses, unintended and unforeseen feedbacks, cross-scale interactions and non-linearities (Magnuszewski *et al.* 2005, Kinzig *et al.* 2006). This complexity makes it difficult to plan and implement policies and management strategies which successfully deliver sustainable resource use in such systems. As a result, the outcomes of traditional environmental management approaches (e.g. control of invasive weeds, revegetation, potentially even provision of environmental flows) applied to these systems are generally poor because they (inevitably) fail to adequately incorporate the elements of system structure that underlie this inherent complexity (Magnuszewski *et al.* 2005).

Decisions about the scale of intervention required to achieve acceptable levels of protection for biodiversity values in these landscapes are often guided by prevailing hypotheses regarding the role these factors play in influencing ecosystem processes and function. However, management approaches derived for systems in one area may not be equally effective in achieving predicted or desired outcomes in different ecological and environmental contexts (Jenkins *et al.* 2005). Increasingly, management must take an adaptive (or experimental) approach with effective monitoring at relevant scales and critical evaluation of approaches to ensure successful return on investment (Folke 2006, Doak *et al.* 2008, Auld and Keith 2009).

8.2.1 Management for ecosystem resilience on the Upper Condamine Floodplain

Native floodplain ecosystems in the Murray-Darling Basin are under stress, particularly those closely associated with the hydrology of the river system (Bramley *et al.* 2003, Overton *et al.* 2006, Doody *et al.* 2009). Research investigating ecosystem response in these systems has centred on the southern MDB along the highly regulated River Murray and its key tributaries. Evidence of declining riverine, wetland and riparian health along these perennially flowing river systems, which are fed by winter-dominant rainfall and snow-melt (Chong and Ladson 2003), is associated with regulation and altered seasonality of flows, raised water tables, increased salinisation and reduced overland flooding (Jolly *et al.* 1993, 1996, Bramley *et al.* 2003, Overton *et al.* 2006). Current management approaches are centred on the restoration of environmental flows designed to mimic historical flow regimes and create overbank flooding to replenish wetlands (Wilson *et al.* 2009) and to reinvigorate riparian and floodplain woodlands by flushing accumulated salts from the system (Doody *et al.* 2009, Overton and Doody 2010). Provision of environmental flows is facilitated through federal government purchase (‘buy back’) of irrigation entitlements, and managed through the release of water from large upstream storages and its distribution through a series of engineered locks and channels at various points within the system (Stewart and Harper 2002, Wen *et al.* 2009).

In many respects, the northern MDB is a different system (Thoms and Sheldon 2002), with natural hydrological regimes governed by a highly variable summer-dominant rainfall pattern characterised by episodic droughts and wet periods (Chapter 2). This results in ephemeral streamflow patterns, with extended no-flow periods and irregular, but occasionally widespread, flooding. There has been limited understanding of key drivers of ecosystem change, and little empirical evidence on which to base environmental flow management decisions, in these highly variable systems (Colloff *et al.* 2010). Water resources in the Upper Condamine are also effectively over-allocated, resulting in an increasingly hydrologically fragmented system (CSIRO 2008). Existing legal entitlements to water in the Upper Condamine are a significant impediment to the provision of water for environmental purposes, and there is currently little scope to address declining floodplain and riparian woodland condition associated with altered hydrological regimes in the Upper Condamine. While water buy-back provides capacity to adjust the levels of water resource allocations and increase the level of environmental flows, the extent to which this will contribute to the protection of flow-dependent (and potentially groundwater-dependent) riverine and riparian environmental assets in a dryland system such as the Condamine-Balonne is unknown (Thoms and Sheldon 2002). Effective environmental flow regimes may be difficult to determine where there is a lack of detailed understanding of the water volumes and dynamics required to maintain ecological function, as is currently the case in the Upper Condamine. There is also limited ecological research from which to predict whether replacing water into riparian environments through environmental flow provisions can redress the already-entrenched, broader impacts of land use (including water use) change (as suggested by this study).

Conversely, the identification of sites at which groundwater is still within the accessible range may form the basis for strategic management of these sites and of groundwater levels in their vicinity. New developments such as the emerging coal seam gas industry in southern Queensland (Moran and Vink 2010) may present opportunities to supplement groundwater levels at high priority sites where appropriate water quality can be assured. In-stream barriers (weirs and large woody debris) which act to slow flows and retain water within the system may offer an opportunity for management to ameliorate the impacts of groundwater decline on tree condition in areas immediately downstream (Chapter 4 and 5).

Other management options to retain remnant riparian woodland condition on the Upper Condamine Floodplain are also not well-supported by current policy or legislative mechanisms. Legislation in Queensland (specifically the *Queensland Vegetation Management Act 1999*) limits (or at least regulates) the further clearing of mapped native ecosystem remnants; however, there is currently little effective control over the management of these, no guarantee regarding their ecological condition, and limited protection for smaller unmapped patches such as narrow riparian remnants. The *Queensland Water Act 2000*, to some extent, restricts the clearing of woody vegetation in watercourses.

There is also little certainty that biodiversity or fundamental ecological values can be retained in remnants embedded in landscapes such as the Upper Condamine floodplain which have already undergone major land use change. Biodiversity planning instruments such as the Queensland Department of Environment and Resource Management (DERM) Biodiversity Assessment Mapping Methodology (BAMM) facilitate the prioritisation of remnant ecosystem protection across landscapes (usually on a bioregional basis; e.g. the Southern Brigalow Belt) and evaluation of development applications. However, they largely fail to address the issue of management under current land uses, or of cumulative off-site impacts of incremental development over time.

Future climate change also adds significant risk and uncertainty (Vervoort 2007), and will increase the complexity of resource management to support water-dependent ecosystems, agricultural production and rural communities in this region. Predictions are that the frequency and intensity of rainfall will change, with a high probability that patterns will become more variable (e.g. longer and more severe drought periods, more intense but less frequent rainfall events; Humphries and Baldwin 2003, Nicholls 2004, IPCC 2007). Catchment modelling indicates that rainfall runoff in the Condamine-Balonne is most likely (60% probability) to decrease by 7 to 20%, while groundwater recharge is predicted to decrease by 10% of recent (1922-1995) levels by 2030 (CSIRO 2008). Improved understanding of interactions and feedbacks in water-dependent ecosystems will enable better prediction of how these additional hydrological disturbances associated with climate change may play out across the Upper Condamine where these systems are close to tipping points, and will contribute to adaptive management approaches to address these new challenges.

8.3 Conclusions and future research directions

In conclusion, it is apparent from this research that riparian *Eucalyptus camaldulensis/E. tereticornis* woodlands on the Upper Condamine floodplain are significantly altered in both extent and condition. They are now effectively highly fragmented novel ecosystems, subject to a range of natural and anthropogenic disturbances including infestation by lippia, a dominant functional alien species, and chronic groundwater decline. It is highly likely that change will continue to occur in this landscape, particularly in conjunction with increasing impacts of climate change. More frequent, intense and longer-duration droughts will have increasing impact as trees lose contact with groundwater which provides a critical buffer during periods of soil moisture deficit. This is likely to result in increasing levels of dieback and mortality in phreatic species such as *Eucalyptus camaldulensis/E. tereticornis.* Associated changes in groundcover composition and functional diversity, and possible expansion of *Acacia stenophylla*, may result in communities which are then much more responsive/susceptible to stochastic climatic events, including episodic flooding, contributing to spiralling degradation. The identification and management of refugia in which there is a higher probability of retaining woodland condition should be investigated as a matter of urgency, while innovative solutions are required to address the fundamental issue of groundwater decline in this landscape.

Inevitably, this research has highlighted the need for further investigation to better understand the mechanisms of ecosystem response of remnant riparian woodlands in this highly modified environment, and a number of additional research questions have already been outlined in individual chapters in this thesis. However, key questions relating to these conclusions are:

(i) How generalisable are these findings to other highly modified systems in the northern Murray Darling Basin and elsewhere?

(ii) What are the potential impacts of climate change in ecosystems already subject to critical changes in disturbance regimes and resource availability due to land use change?

(iii) How can ecological knowledge and understanding of ecosystem change be effectively and efficiently incorporated into adaptive management programs?

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Appendix A Survey site details

Sites	Site code	Northing	Easting	Riversection	Riverbank[1]	Landuse[2]
1	TY1	6916714	364376	Upper	R	G
2	TY2	6915422	364354	Upper	L	G
3	TY4	6913161	367678	Upper	R	G
4	TY5	6912960	367513	Upper	R	G
5	TY6	6910137	370979	Upper	R	G
6	TY7	6918018	360501	Upper	R	U
7	TY8	6914561	362364	Upper	L	U
8	TY9	6916180	354168	Upper	L	G
9	YL1	6926808	336447	Middle	R	U
10	YL2	6928226	334443	Middle	R	U
11	YL3	6923042	338454	Middle	L	U
12	YL4	6925730	336847	Middle	R	G
13	YL5	6925130	337517	Middle	R	G
14	YL6	6924934	337264	Middle	L	G
15	YL8	6922154	339436	Middle	L	U
16	YL9	6920424	341771	Middle	L	U
17	YL10	6920925	341039	Middle	R	U
18	LC1	6929625	332214	Lower	R	U
19	LC3	6931932	329910	Lower	L	U
20	LC4	6932937	328811	Lower	L	U
21	LC5	6930635	331179	Lower	R	U
22	LC6	6952213	322236	Lower	L	G
23	LC7	6949730	321029	Lower	R	U
24	LC8	6932132	330179	Lower	R	U
REF1	OT1	6899162	379985	-	L	U
REF2	TL1	6975430	325667	-	R	U
REF3	TL2	6975310	326271	-	R	U

[1] Riverbanks (L: left, R: right); [2] Landuse (G: grazed, U: ungrazed)

Appendix B Functional group classifications for species recorded on the Upper Condamine floodplain (27 sites)

Species	**Family**	**Metabolism**	**Lifecycle**	**Life-form**	**di/monocot**	**clonal**	**native**	**Habitat**	**Reference**
Acacia stenophylla	Fabaceae	C3	perennial	tree	Dicot	no	native	wetland & floodplain	http://www.anbg.gov.au/angio/legumino.htm
Alternanthera denticulata	Amaranthaceae	C3	annual	forb	Dicot	clonal	native	floodplain	http://www.anbg.gov.au/angio/amaranth.htm
Alternanthera nodiflora	Amaranthaceae	C3	annual	forb	Dicot	clonal	native	floodplain	http://www.anbg.gov.au/angio/amaranth.htm
Ammi majus	Apiaceae	C3	short-lived	forb	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/umbellif.htm
Angophora floribunda	Myrtaceae	C3	perennial	tree	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/myrtacea.htm
Aristida leptopoda	Poaceae	C4	perennial	tussock grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Aristida ramosa	Poaceae	C4	perennial	tussock grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Asparagus virgatus	Asparagaceae	C3	perennial	vine	Monocot	no	alien	terrestrial	http://www.anbg.gov.au/angio/asparaga.htm
Asperula conferta	Rubiaceae	C3	perennial	forb	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/rubiacea.htm
Austrostipa scabra	Poaceae	C3	perennial	tussock grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Austrostipa setacea	Poaceae	C3	perennial	tussock grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Austrostipa verticillata	Poaceae	C3	perennial	tussock grass	Monocot	clonal	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Avena barbata	Poaceae	C3	annual	grass	Monocot	no	alien	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Bidens pilosa.	Asteraceae	C3	annual	forb	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/composit.htm
Boerhavia dominii	Nyctaginaceae	C4	perennial	forb	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/nyctagin.htm
Bothriochloa biloba	Poaceae	C4	perennial	tussock grass	Monocot	no	native	floodplain	Sharp & Simon 2001
Bothriochloa decipiens	Poaceae	C4	perennial	tussock grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Bothriochloa ewartiana.	Poaceae	C4	perennial	tussock grass	Monocot	no	native	terrestrial	Sharp & Simon 2002
Brassicaceae spp.	Brassicaceae	C3	annual	forb	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/crucifer.htm
Bromus catharticus	Poaceae	C3	short-lived	tussock grass	Monocot	no	alien	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Bromus inermis	Poaceae	C3	perennial	grass	Monocot	clonal	alien	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Brunoniella australis.	Acanthaceae	C3	perennial	forb	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/acanthac.htm
Bulbine bulbosa	Asphodelaceae	C3	perennial	forb	Monocot	no	native	terrestrial	http://www.anbg.gov.au/angio/asphodel.htm
Calotis cuneata var. cuneata	Asteraceae	-	perennial	forb	Dicot	clonal	native	terrestrial	http://www.anbg.gov.au/angio/composit.htm
Carex inversa	Cyperaceae	C3	perennial	forb	Monocot	clonal	native	terrestrial	Liu & Wang 2006; Bruhl & Wilson 2007
Chamaesyce drummondii	Euphorbiaceae	C4	perennial	forb	Dicot	clonal	native	terrestrial	http://www.anbg.gov.au/angio/euphorbi.htm

Species	Family	Metabolism	Lifecycle	Life-form	di/monocot	clonal	native	Habitat	Reference
Chenopodium auricomiforme	Chenopodiaceae	C3	short-lived	chenopod shrub	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/chenopod.htm
Chenopodium auricomum	Chenopodiaceae	C3	perennial	chenopod shrub	Dicot	no	native	wetland & floodplain	http://www.anbg.gov.au/angio/chenopod.htm
Chloris divaricata	Poaceae	C4	perennial	tussock grass	Monocot	clonal	native	floodplain	Watson & Dallwitz 1980; Sharp & Simon 2002
Chloris gayana	Poaceae	C4	perennial	grass	Monocot	clonal	alien	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Chloris truncata	Poaceae	C4	perennial	grass	Monocot	clonal	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Chloris ventricosa	Poaceae	C4	perennial	grass	Monocot	clonal	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Cichorium intybus	Asteraceae	C3	perennial	forb	Dicot	no	alien	terrestrial	Fitter & Peat 1994
Cirsium vulgare	Asteraceae	C3	short-lived	forb	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/composit.htm
Commelina cyanea	Commelinaceae	C3	perennial	forb	Monocot	no	native	terrestrial	http://www.anbg.gov.au/angio/commelin.htm
Conyza bonariensis	Asteraceae	C3	annual	forb	Dicot	no	alien	terrestrial	http://www.rcia.puc.cl/English/pdf/34-1/SFeldman1.pdf
Corymbia tessellaris	Myrtaceae	C3	perennial	tree	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/myrtacea.htm
Cyclospermum leptophyllum	Apiaceae	C3	annual	forb	Dicot	no	alien	riparian & floodplain	McIntyre *et al.* 2005
Cymbopogon refractus	Poaceae	C4	perennial	tussock grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Cynodon dactylon	Poaceae	C4	perennial	grass	Monocot	clonal	native	terrestrial	Watson & Dallwitz 1980
Cynoglossum suaveolens	Boraginaceae	C3	short-lived	forb	Dicot	no	native	terrestrial	Watson & Dallwitz 1992
Cyperus gracilis.	Cyperaceae	C3	perennial	sedge	Monocot	no	native	terrestrial	Bruhl & Wilson (in press)
Cyperus gunnii	Cyperaceae	C4	perennial	sedge	Monocot	clonal	native	wetland & floodplain	Bruhl & Wilson (in press)
Cyperus vaginatus	Cyperaceae	C3	perennial	sedge	Monocot	clonal	native	riparian	Bruhl & Wilson (in press)
Dianella sp.	Phormiaceae	-	perennial	forb	Monocot	no	native	terrestrial	http://www.anbg.gov.au/angio/phormiac.htm
Dichanthium sericeum	Poaceae	C4	perennial	grass	Monocot	no	native	terrestrial	Sharp & Simon 2002
Digitaria brownii	Poaceae	C4	perennial	grass	Monocot	clonal	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Digitaria divaricatissima	Poaceae	C4	perennial	tussock grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Einadia hastata	Chenopodiaceae	C3	perennial	chenopod shrub	Dicot	no	native	floodplain	http://www.anbg.gov.au/angio/chenopod.htm
Einadia nutans	Chenopodiaceae	C3	perennial	chenopod shrub	Dicot	no	native	floodplain	http://www.anbg.gov.au/angio/chenopod.htm
Einadia polygonoides	Chenopodiaceae	C3	short-lived	chenopod shrub	Dicot	no	native	floodplain	http://www.anbg.gov.au/angio/chenopod.htm
Einadia trigonos	Chenopodiaceae	C3	perennial	chenopod shrub	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/chenopod.htm
Eleocharis acuta	Cyperaceae	C3	perennial	sedge	Monocot	clonal	native	wetland & floodplain	Takeda *et al.* 1985
Elymus multiflorus	Poaceae	C3	perennial	tussock grass	Monocot	no	native	floodplain	Watson & Dallwitz 1980; Sharp & Simon 2002

Species	**Family**	**Metabolism**	**Lifecycle**	**Life-form**	**di/monocot**	**clonal**	**native**	**Habitat**	**Reference**
Elymus scaber	Poaceae	C3	perennial	tussock grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Enneapogon nigricans	Poaceae	C4	short-lived	tussock grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Eragrostis leptostachya	Poaceae	C4	perennial	tussock grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Eriochloa procera	Poaceae	C4	perennial	tussock grass	Monocot	no	native	floodplain	Sharp & Simon 2001
Eriochloa pseudoacrotricha	Poaceae	C4	short-lived	tussock grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Eucalyptus camaldulensis	Myrtaceae	C3	perennial	tree	Dicot	no	native	riparian & floodplain	http://www.anbg.gov.au/angio/myrtacea.htm
Eucalyptus populnea	Myrtaceae	C3	perennial	tree	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/myrtacea.htm
Eucalyptus tereticornis	Myrtaceae	C3	perennial	tree	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/myrtacea.htm
Eulalia aurea	Poaceae	C4	perennial	grass	Monocot	clonal	native	floodplain	Watson & Dallwitz 1980; Sharp & Simon 2002
Eustrephus latifolius.	Philesiaceae	-	perennial	vine	Monocot	no	native	terrestrial	http://www.anbg.gov.au/angio/luzuriag.htm
Glandularia aristigera.	Verbenaceae	C3	perennial	forb	Dicot	clonal	alien	terrestrial	http://www.anbg.gov.au/angio/verbenac.htm
Gleditsia triacanthos	Caesalpiniaceae	C3	perennial	tree	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/legumino.htm
Glycine latifolia	Fabaceae	C3	perennial	forb	Dicot	clonal	native	terrestrial	http://www.anbg.gov.au/angio/legumino.htm
Glycine tabacina	Fabaceae	C3	perennial	forb	Dicot	clonal	native	terrestrial	http://www.anbg.gov.au/angio/legumino.htm
Glycine tomentella	Fabaceae	C3	perennial	forb	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/legumino.htm
Gnaphalium sphaericum	Asteraceae	C3	annual	forb	Dicot	no	native	terrestrial	Liu & Wang 2006
Gomphocarpus physocarpus	Asclepiadaceae	C3	perennial	forb	Dicot	no	alien	terrestrial	McIntyre *et al.* 2005
Haloragis stricta	Haloragidaceae	C3	perennial	forb	Dicot	no	native	wetland & floodplain	http://delta-intkey.com/angio/www/haloragi.htm
Hibiscus trionum	Malvaceae	C3	short-lived	shrub	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/malvacea.htm
Jasminum simplicifolium	Oleaceae	C3	perennial	vine	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/juncacea.htm
Juncus sp.	Juncaceae	C3	perennial	rush	Monocot	clonal	native	-	http://www.anbg.gov.au/angio/juncacea.htm
Lactuca serriola	Asteraceae	C3	short-lived	forb	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/composit.htm
Lepidium africanum	Brassicaceae	C3	annual	forb	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/crucifer.htm
Lepidium bonariense	Brassicaceae	C3	short-lived	forb	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/crucifer.htm
Lepidium pseudohyssopifolium	Brassicaceae	C3	short-lived	forb	Dicot	no	native	floodplain	http://www.anbg.gov.au/angio/crucifer.htm
Leptochloa divaricatissima	Poaceae	C4	perennial	tussock grass	Monocot	no	native	floodplain	Watson & Dallwitz 1980; Sharp & Simon 2002
Leptochloa fusca	Poaceae	C4	short-lived	tussock grass	Monocot	no	native	terrestrial	Sharp & Simon 2002
Lomandra longifolia	Lomandraceae	-	perennial	rush	Monocot	no	native	terrestrial	-

Species	Family	Metabolism	Lifecycle	Life-form	di/monocot	clonal	native	Habitat	Reference
Lomandra multiflora	Lomandraceae	-	perennial	rush	Monocot	no	native	terrestrial	-
Maireana microphylla	Chenopodiaceae	C3	perennial	chenopod shrub	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/chenopod.htm
Malvastrum americanum	Malvaceae	C3	short-lived	forb	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/malvacea.htm
Malvastrum coromandelianum	Malvaceae	C3	short-lived	forb	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/malvacea.htm
Marsilea sp.	Marsileaceae	-	perennial	fern	Fern Ally	clonal	native	wetland & floodplain	-
Megathyrsus maximus	Poaceae	C4	perennial	tussock grass	Monocot	clonal	alien	terrestrial	McIntyre *et al.* 2005
Mentha satureioides	Lamiaceae	C3	perennial	forb	Dicot	clonal	native	terrestrial	Liu & Wang 2006
Modiola caroliniana	Malvaceae	C3	short-lived	forb	Dicot	clonal	alien	terrestrial	http://www.anbg.gov.au/angio/malvacea.htm
Neptunia gracilis	Mimosaceae	C3	perennial	forb	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/legumino.htm
Notodanthonia longifolia	Poaceae	C3	perennial	tussock grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Opuntia aurantiaca	Cactaceae	CAM	perennial	cactus	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/cactacea.htm
Opuntia stricta	Cactaceae	CAM	perennial	cactus	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/cactacea.htm
Opuntia tomentosa	Cactaceae	CAM	perennial	cactus	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/cactacea.htm
Oxalis perennans	Oxalidaceae	C3 or CAM	perennial	forb	Dicot	clonal	native	terrestrial	http://www.anbg.gov.au/angio/oxalidac.htm
Panicum antidotale	Poaceae	C3/C4 (variable)	perennial	tussock grass	Monocot	clonal	alien	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Panicum buncei	Poaceae	C3/C4 (variable)	perennial	tussock grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Panicum decompositum	Poaceae	C3/C4 (variable)	perennial	tussock grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Panicum effusum	Poaceae	C3/C4 (variable)	perennial	tussock grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Panicum larcomianum	Poaceae	C3/C4 (variable)	perennial	grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Panicum queenslandicum	Poaceae	C3/C4 (variable)	perennial	tussock grass	Monocot	no	native	floodplain	Watson & Dallwitz 1980; Sharp & Simon 2002
Paspalidium aversum	Poaceae	C4	perennial	tussock grass	Monocot	no	native	floodplain	Watson & Dallwitz 1980; Sharp & Simon 2002
Paspalidium globoideum	Poaceae	C4	perennial	tussock grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Paspalum dilatatum	Poaceae	C4	perennial	tussock grass	Monocot	no	alien	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Pavonia hastata	Malvaceae	C3	perennial	shrub	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/malvacea.htm
Pennisetum clandestinum	Poaceae	C4	perennial	grass	Monocot	clonal	alien	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Phalaris minor	Poaceae	C3	annual	tussock grass	Monocot	no	alien	terrestrial	Sharp & Simon 2002
Phyla canescens	Verbenaceae	C3	perennial	forb	Dicot	clonal	alien	floodplain	http://www.anbg.gov.au/angio/verbenac.htm
Phyllanthus virgatus	Euphorbiaceae	C3	perennial	forb	Dicot	no	native	riparian & floodplain	http://www.anbg.gov.au/angio/euphorbi.htm

Species	**Family**	**Metabolism**	**Lifecycle**	**Life-form**	**di/monocot**	**clonal**	**native**	**Habitat**	**Reference**
Pimelea neo-anglica	Thymelaceae	C3	perennial	shrub	Dicot	no	native	terrestrial	http://delta-intkey.com/angio/www/thymelae.htm
Plantago debilis	Plantaginaceae	C3	short-lived	forb	Dicot	no	native	riparian & floodplain	http://www.anbg.gov.au/angio/plantagi.htm
Portulaca oleracea	Portulacaceae	C4 or CAM	short-lived	forb	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/portulac.htm
Rhynchosia minima	Fabaceae	C3	perennial	forb	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/legumino.htm
Rostellularia adscendens	Acanthaceae	C3	perennial	forb	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/acanthac.htm
Rumex brownii	Polygonaceae	C3	perennial	forb	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/polygona.htm
Rumex crispus	Polygonaceae	C3	perennial	forb	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/polygona.htm
Salsola tragus	Chenopodiaceae	C3 or C4	short-lived	chenopod shrub	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/chenopod.htm
Salvia reflexa	Lamiaceae	C3	annual	forb	Dicot	no	alien	floodplain	Leonardos & Grodzinski 2000
Salvia verbenaca	Lamiaceae	C3	perennial	forb	Dicot	no	alien	terrestrial	Leonardos & Grodzinski 2000
Scleria sp.	Cyperaceae	C3	perennial	forb	Monocot	clonal	-	wetland & floodplain	http://www.springerlink.com/content/d863771751168284/fulltext.pdf
Sclerolaena birchii	Chenopodiaceae	C3	perennial	chenopod shrub	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/chenopod.htm
Sclerolaena muricata var. muricata	Chenopodiaceae	C3	perennial	chenopod shrub	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/chenopod.htm
Sclerolaena muricata var. semiglabra	Chenopodiaceae	C3	perennial	chenopod shrub	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/chenopod.htm
Sclerolaena muricata var. villosa	Chenopodiaceae	C3	perennial	chenopod shrub	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/chenopod.htm
Senecio quadridentatus	Asteraceae	CAM or C3	perennial	forb	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/composit.htm
Senna barclayana	Caesalpiniaceae	C3	perennial	forb	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/legumino.htm
Setaria distans	Poaceae	C4	perennial	tussock grass	Monocot	no	native	terrestrial	Sharp & Simon 2002
Setaria jubiflora	Poaceae	C4	perennial	tussock grass	Monocot	no	native	riparian & floodplain	Sharp & Simon 2002
Setaria pumila	Poaceae	C4	annual	tussock grass	Monocot	no	alien	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Sida filiformis	Malvaceae	C3	perennial	forb	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/malvacea.htm
Sida rhombifolia	Malvaceae	C3	perennial	forb	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/malvacea.htm
Sida subspicata	Malvaceae	C3	perennial	forb	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/malvacea.htm
Solanum americanum	Solanaceae	C3	short-lived	forb	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/solanace.htm
Sonchus oleraceus	Asteraceae	C3	annual	forb	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/composit.htm
Sorghum halepense	Poaceae	C4	perennial	grass	Monocot	clonal	alien	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Sporobolus creber	Poaceae	C4	perennial	tussock grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Sporobolus elongatus	Poaceae	C4	perennial	tussock grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002

Species	**Family**	**Metabolism**	**Lifecycle**	**Life-form**	**di/monocot**	**clonal**	**native**	**Habitat**	**Reference**
Swainsona sp.	Fabaceae	C3	short-lived	forb	Dicot	no	native	riparian & floodplain	http://www.anbg.gov.au/angio/legumino.htm
Tagetes minuta	Asteraceae	C3	annual	forb	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/composit.htm
Taraxacum officinale	Asteraceae	C3	perennial	forb	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/composit.htm
Themeda avenacea	Poaceae	C4	perennial	grass	Monocot	no	native	floodplain	Watson & Dallwitz 1980; Sharp & Simon 2002
Themeda triandra	Poaceae	C4	perennial	tussock grass	Monocot	no	native	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Tribulus terrestris	Zygophyllaceae	C4	annual	forb	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/zygophyl.htm
Urochloa panicoides	Poaceae	C4	annual	grass	Monocot	clonal	alien	terrestrial	Watson & Dallwitz 1980; Sharp & Simon 2002
Vachellia farnesiana	Mimosaceae	C3	perennial	shrub	Dicot	no	native	floodplain	http://www.anbg.gov.au/angio/legumino.htm
Verbena officinalis	Verbenaceae	C3	perennial	forb	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/verbenac.htm
Vicia sp.	Fabaceae	C3	annual	forb	Dicot	no	alien	terrestrial	http://www.anbg.gov.au/angio/legumino.htm
Vittadinia cuneata var. hirsuta	Asteraceae	-	short-lived	forb	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/composit.htm
Vittadinia pterochaeta	Asteraceae	-	annual	forb	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/composit.htm
Wahlenbergia communis	Campanulaceae	C3	perennial	forb	Dicot	no	native	terrestrial	http://www.anbg.gov.au/angio/campanul.htm
Walwhalleya subxerophila	Poaceae	C3	perennial	tussock grass	Monocot	no	native	floodplain	Sharp & Simon 2002

Appendix C Species frequency data, Upper Condamine floodplain (27 sites)

River Section		**Upper**								**Middle**									**Lower**								
Sites	**R1**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**R2**	**R3**
Species																											
Acacia stenophylla	0	0	0	0	0	0	2	0	0	1	0	0	0	1	0	0	0	1	3	1	2	2	1	0	2	1	1
Alternanthera denticulata	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Alternanthera nodiflora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Ammi majus	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Angophora floribunda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Aristida leptopoda	0	0	0	1	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aristida ramosa	5	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	7	3	0	1	6
Asparagus virgatus	2	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Asperula conferta	2	2	5	1	2	0	2	7	0	0	7	0	4	1	2	0	0	0	3	0	0	0	0	0	0	0	0
Austrostipa scabra	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Austrostipa setacea	7	2	0	1	2	7	1	2	0	0	0	0	0	1	0	0	5	0	0	0	2	1	0	0	0	0	0
Austrostipa verticillata	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Avena barbata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Bidens pilosa	5	0	0	2	1	0	2	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	0
Boerhavia dominii	0	0	0	0	2	0	5	0	0	0	0	0	0	2	0	0	0	0	0	0	1	1	0	0	0	0	0
Bothriochloa biloba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Bothriochloa decipiens	0	0	0	1	0	0	1	0	0	0	0	0	1	6	0	0	0	0	0	0	7	0	2	0	0	0	0
Bothriochloa ewartiana	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brassica sp.	0	4	0	0	0	3	1	0	4	2	2	1	2	3	1	4	3	3	3	6	2	6	0	0	4	0	0
Bromus catharticus	2	0	0	0	0	0	2	0	4	0	3	0	0	0	0	6	2	0	0	6	0	1	0	0	0	0	0
Bromus inermis	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Brunoniella australis	0	1	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	5	2	0	0	3	0	2
Bulbine sp.	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	4	0	2	0	0	0	0	0
Calotis cuneata var. cuneata	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex inversa	7	7	0	0	0	0	3	5	0	2	1	5	1	1	0	0	2	0	2	5	2	2	0	6	0	2	6
Chamaesyce drummondii	0	4	0	3	4	0	0	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chenopodium auricomiforme	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Chenopodium auricomum	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Chloris divaricata	0	0	0	2	6	0	2	1	0	0	0	0	2	0	0	2	3	0	1	0	0	3	5	0	0	3	1
Chloris gayana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Chloris truncata/ventricosa	0	5	0	1	0	1	1	0	0	0	0	0	2	6	0	0	0	0	0	0	1	0	0	4	0	2	3

River Section		**Upper**								**Middle**									**Lower**								
Sites	**R1**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**R2**	**R3**
Cichorium intybus	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cirsium vulgare	2	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Commelina cyanea	5	5	2	1	1	0	5	3	0	0	1	0	0	1	0	0	2	0	3	2	1	6	0	1	3	0	0
Conyza bonariensis	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	5	0	0	0	0	3	0	0	1	0	0
Corymbia tessellaris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Cyclospermum leptophyllum	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	2	0	1	1	0	3	0	0	0	1	0
Cymbopogon refractus	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Cynodon dactylon	3	2	0	4	0	2	7	0	5	0	0	0	1	7	0	3	0	1	7	7	2	7	7	0	4	0	0
Cynoglossum suaveolens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Cyperus gracilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0
Cyperus gunnii	2	1	7	1	7	2	3	5	1	7	6	7	7	5	7	1	7	3	7	7	0	3	4	1	1	4	2
Cyperus vaginatus	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dianella sp.	2	2	0	0	0	0	0	3	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	2
Dichanthium sericeum	6	7	4	7	7	1	2	7	2	1	0	4	7	7	2	3	5	3	3	2	2	2	7	1	3	3	7
Digitaria brownii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Digitaria divaricatissima	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0
Einadia hastata/trigonos	7	1	1	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Einadia nutans/polygonoides	2	7	5	3	1	2	7	9	1	3	1	3	5	4	0	8	7	11	7	5	9	7	4	2	6	7	5
Eleocharis acuta	0	0	0	1	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0
Elymus multiflorus	2	5	3	3	0	1	2	2	3	6	3	3	1	3	1	1	6	6	5	7	5	3	5	1	3	1	0
Elymus scaber	0	0	4	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Enneapogon nigricans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
epiphytic orchid	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Eragrostis leptostachya	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Eriochloa pseudoacrotricha/procera	0	5	0	3	5	0	3	3	0	3	0	4	7	6	3	7	7	3	0	0	7	3	3	3	5	2	6
Eucalyptus camaldulensis/tereticornis	2	1	2	2	2	1	2	1	3	1	2	2	2	3	1	1	3	2	2	2	1	0	2	3	2	3	2
Eucalyptus populnea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Eulalia aurea	1	5	7	7	3	2	0	2	0	1	2	0	1	4	3	0	3	0	3	3	2	0	3	2	2	0	0
Eustrephus latifolius	3	0	0	0	0	0	1	3	1	0	2	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	1
Glandularia aristigera	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	3
Gleditsia triacanthos	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glycine latifolia	0	0	0	0	4	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glycine tabacina	3	0	1	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	4	2	0	1	0	1	0
Glycine tomentella	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

River Section		**Upper**								**Middle**									**Lower**								
Sites	**R1**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**R2**	**R3**
Gnaphalium sphaericum	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gomphocarpus physocarpus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Haloragis stricta	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hibiscus trionum	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
Jasminum simplicifolium	7	4	3	0	1	0	0	3	1	0	0	0	2	0	0	0	0	0	0	2	0	0	0	2	0	0	0
Juncus sp.	0	0	7	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Lactuca serriola	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Lepidium africanum/bonariense	0	1	0	1	0	0	3	1	0	1	0	0	4	2	1	0	1	4	1	3	0	5	0	1	0	2	0
Lepidium pseudohyssopifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	1	0	1	0	6	0	0
Leptochloa divaricatissima	0	0	0	2	0	0	7	0	0	1	0	0	5	0	0	7	3	0	7	7	7	7	0	2	7	3	1
Leptochloa fusca	2	0	1	0	0	1	5	0	0	1	7	2	0	0	1	0	2	2	1	5	1	0	0	0	3	0	0
Lomandra longifolia	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Lomandra multiflora	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0
Maireana microphylla	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Malvastrum americanum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Malvastrum coromandelianum	0	0	0	0	0	0	0	0	2	0	0	0	2	1	0	3	0	0	0	0	0	0	1	0	0	3	0
Marsilea sp.	3	0	6	3	0	3	6	7	7	3	4	2	3	0	6	1	2	4	4	1	0	0	5	3	0	1	3
Megathyrsus maximus	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Mentha satureioides	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiola caroliniana	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neptunia gracilis	0	4	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Notodanthonia longifolia	0	5	2	3	5	1	1	2	0	0	0	0	2	2	0	1	5	0	0	0	0	0	0	3	0	1	0
Opuntia aurantiaca	0	0	0	0	0	2	0	0	1	0	0	0	0	3	0	0	6	0	2	0	2	6	0	0	1	1	2
Opuntia stricta	0	0	0	0	0	2	1	3	0	1	0	0	1	0	0	0	2	0	0	0	3	2	0	0	2	1	3
Opuntia tomentosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Oxalis perennans	3	2	1	0	1	0	0	0	1	0	0	2	1	2	0	0	0	0	1	3	0	1	0	0	0	2	0
Panicum antidotale	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Panicum buncei	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Panicum decompositum	0	0	0	3	7	1	2	0	0	4	0	4	0	0	7	0	7	0	0	3	0	3	0	0	0	0	0
Panicum effusum	0	0	0	6	2	0	0	0	0	0	0	3	0	5	2	0	5	0	0	0	0	0	2	0	0	0	0
Panicum larcomianum	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	2	0	0	0	2
Panicum queenslandicum	0	6	6	0	2	0	0	7	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	7	6
Paspalidium aversum	3	4	0	7	7	0	0	4	0	0	3	0	0	5	0	0	4	1	6	2	0	7	6	0	0	3	4
Paspalidium globoideum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0

River Section		**Upper**								**Middle**									**Lower**								
Sites	**R1**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**R2**	**R3**
Paspalum dilatatum	7	0	3	3	1	0	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Pavonia hastata	2	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Pennisetum clandestinum	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phalaris minor	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyla canescens	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	4	7	7	7	4	7
Phyllanthus virgatus	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Pimelea neoanglica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Plantago debilis	0	0	0	2	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Portulaca oleracea	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	3	1	0	0	0	0	0	0	0	0	3	2
Rhynchosia minima	0	2	0	3	5	0	0	4	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Rostellularia adscendens	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rumex brownii	3	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0
Rumex crispus	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salsola tragus	0	2	2	3	0	0	2	0	2	0	0	0	1	1	0	2	2	1	0	0	0	3	0	0	0	5	2
Salvia reflexa	0	1	0	0	0	3	4	0	0	0	0	0	2	2	0	3	1	7	0	0	0	6	0	0	0	2	1
Salvia verbenaca	0	0	0	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scleria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sclerolaena birchii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0
Sclerolaena muricata var. muricata	0	6	0	1	0	0	1	0	0	1	0	0	3	7	0	4	3	2	0	1	2	7	2	2	4	0	0
Sclerolaena muricata var. semiglabra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	3	0
Sclerolaena muricata var. villosa	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Senecio quadridentatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Senna barclayana	0	0	0	4	2	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Setaria distans	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	5	0	0	5	5	1	0	0
Setaria jubiflora	0	0	0	0	0	0	5	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	6	0
Setaria pumila	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Sida filiformis	0	1	0	0	0	2	0	1	0	0	0	0	2	0	0	1	0	0	0	1	0	0	0	0	1	0	0
Sida rhombifolia	7	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Sida subspicata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Solanum americanum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Sonchus oleraceus	0	0	1	0	0	1	2	0	0	1	0	0	1	1	0	0	0	0	3	3	0	4	0	0	0	0	0
Sorghum halepense	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sporobolus creber	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Sporobolus elongatus	0	0	0	0	0	0	0	0	3	0	0	0	1	5	0	0	0	0	0	0	0	1	0	0	0	0	0

River Section		**Upper**								**Middle**									**Lower**								
Sites	**R1**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**R2**	**R3**
Swainsona sp. 1	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	2
Tagetes minuta	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Taraxacum officinale	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Themeda avenacea	0	4	4	5	3	0	1	1	0	0	0	0	7	5	1	0	7	0	2	2	4	0	0	0	2	0	0
Themeda triandra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Tribulus terrestris	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
Urochloa panicoides	1	0	1	3	3	3	2	0	2	0	0	0	1	1	0	3	5	2	0	0	0	2	2	0	0	0	0
Vachellia farnesiana	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1
Verbena officinalis	3	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vicia sp. 1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vittadinia cuneata var. hirsuta	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vittadinia pterochaeta	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Wahlenbergia communis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Walwhalleya subxerophila	0	0	0	0	0	0	3	0	0	4	2	0	0	0	0	5	0	7	3	0	0	0	0	0	0	0	0

Appendix D Environmental variables assessed for use in community composition and condition response modelling. Detailed explanations are provided for variable terms, and means, standard errors and minimum and maximum values for each variable (27 sites) are presented.

Environmental variable	**Details**	**units**	**n**	**Mean**	**SE**	**Minimum**	**Maximum**
allcropppn500	proportion of cropping land use[1] (all cropping categories; by area) within 500 m buffer	-	27	0.42	0.04	0.02	0.80
allcropppn2000	proportion of cropping land use[1] (all cropping categories; by area) within 2000 m buffer	-	27	0.69	0.03	0.26	0.91
allcropppn5000	proportion of cropping land use[1] (all cropping categories; by area) within 5000 m buffer	-	27	0.72	0.03	0.34	0.87
allcropppnUQ500	proportion of cropping land use[1] (all cropping categories; by area) within upslope quadrant to 500 m	-	27	0.49	0.06	0.00	0.92
allcropppnUQ2000	proportion of cropping land use[1] (all cropping categories; by area) within upslope quadrant to 2000 m	-	27	0.69	0.04	0.07	0.92
allcropppnUQ5000	proportion of cropping land use[1] (all cropping categories; by area) within upslope quadrant to 5000 m	-	27	0.72	0.04	0.01	0.95
bareground	mean percent cover of bare ground per site (1m x 1m quadrats; Ch.3)	%	27	5.41	1.38	0.00	22.50
cropnatratio500	dominant land use[1] (ratio all cropping :'natural' land use categories) within 500 m buffer	-	27	1.11	0.19	0.02	3.90
cropnatratio2000	dominant land use[1] (ratio all cropping :'natural' land use categories) within 2000 m buffer	-	27	3.49	0.46	0.36	10.69
cropnatratio5000	dominant land use[1] (ratio all cropping :'natural' land use categories) within 5000 m buffer	-	27	4.09	0.46	0.55	8.19
cropnatratioUQ500	dominant land use[1] (ratio all cropping :'natural' land use categories) within upslope quadrant to 500 m	-	27	2.22	0.52	0.00	11.96
cropnatratioUQ2000	dominant land use[1] (ratio all cropping :'natural' land use categories) within upslope quadrant to 2000 m	-	27	4.34	0.73	0.08	12.87
cropnatratioUQ5000	dominant land use[1] (ratio all cropping :'natural' land use categories) within upslope quadrant to 5000 m	-	27	7.54	1.59	0.02	31.41
distupweir	distance from the nearest in-stream weir upstream of a site	km	27	12.90	1.45	1.69	26.64
distdownweir	distance from the nearest in-stream weir downstream of a site	km	27	10.62	1.42	0.17	24.82
distedgeRE	distance from the mapped edge of ecosystem remnant[2]	m	27	70.96	27.87	-221.02	501.56
distGWprodbore	distance from the nearest existing registered groundwater irrigation/production bore[3]	m	27	1706.70	228.22	176.00	5000.00
disthardedge	distance from the nearest natural vegetation edge adjacent to cropping land use[1]	m	27	155.96	26.82	12.66	562.20
distringtankUQ	distance from the nearest upslope ring tank[4]	m	27	3065.56	437.04	104.00	7791.00

Environmental variable	**Details**	**units**	**n**	**Mean**	**SE**	**Minimum**	**Maximum**
distriv	distance to main river channel or mapped tributary[5]	m	27	119.30	16.97	5.00	373.00
drainage500	length of river channel/mapped drainage lines[5] within 500 m buffer	km	27	1.52	0.09	0.73	2.42
drainage2000	length of river channel/mapped drainage lines[5] within 2000 m buffer	km	27	9.43	0.72	5.02	17.18
drainage5000	length of river channel/mapped drainage lines[5] within 5000 m buffer	km	27	41.66	4.18	14.63	77.57
east	easting[6]	-	27	343801.19	3291.44	321029.00	379985.00
elev	elevation[6]	masl	27	390.33	3.29	360.00	422.00
grazppn500	proportion of grazing land use[1] (by area) within 500 m buffer	-	27	0.22	0.06	0.00	0.87
grazppn2000	proportion of grazing land use[1] (by area) within 2000 m buffer	-	27	0.16	0.03	0.00	0.70
grazppn5000	proportion of grazing land use[1] (by area) within 5000 m buffer	-	27	0.18	0.03	0.03	0.60
grazppnUQ500	proportion of grazing land use[1] (by area) within upslope quadrant to 500 m	-	27	0.20	0.06	0.00	1.00
grazppnUQ2000	proportion of grazing land use[1] (by area) within upslope quadrant to 2000 m	-	27	0.15	0.04	0.00	0.92
grazppnUQ5000	proportion of grazing land use[1] (by area) within upslope quadrant to 5000 m	-	27	0.19	0.05	0.00	0.94
GW2000	number of existing registered groundwater bores[3] within 2000 m buffer	-	27	6.26	0.91	1.00	18.00
GW5000	number of existing registered groundwater bores[3] within 5000 m buffer	-	27	55.81	2.49	17.00	78.00
GWalloc2000	total groundwater allocation of licensed bores[3] within 2000 m buffer	ML	27	624.12	131.66	0.00	2850.00
GWalloc5000	total groundwater allocation of licensed bores[3] within 5000 m buffer	ML	27	7539.70	895.98	674.00	18426.00
GWdepth5000	mean depth to water table (averaged over 2004-5 records) for groundwater monitoring bores[3] within 5000 m buffer	m	27	15.46	0.67	9.08	19.63
GWirrig5000	number of existing registered groundwater irrigation bores[3] within 5000 m buffer	-	27	17.48	1.47	3.00	37.00
GWprod2000	number of existing registered & licensed groundwater bores[3] within 2000 m buffer	-	27	2.37	0.55	0.00	13.00
GWprod5000	number of existing registered & licensed groundwater bores[3] within 5000 m buffer	-	27	19.41	1.47	5.00	39.00
GWstk5000	number of existing registered & unlicensed (stock & domestic) groundwater bores[3] within 5000 m buffer	-	27	2.44	0.44	0.00	8.00
GWtrend5000	mean trend in water level of groundwater monitoring bores[3] within 5000 m buffer	m/decade	27	-0.79	0.09	-0.02	-1.81
irrigcropppn500	proportion of irrigated cropping land use[1] (by area) within 500 m buffer	-	27	0.07	0.03	0.00	0.41
irrigcropppn2000	proportion of irrigated cropping land use[1] (by area) within 2000 m buffer	-	27	0.20	0.03	0.02	0.65

Environmental variable	Details	units	n	Mean	SE	Minimum	Maximum
irrigcropppn5000	proportion of irrigated cropping land use[1] (by area) within 5000 m buffer	-	27	0.25	0.01	0.14	0.38
irrigcropppnUQ500	proportion of irrigated cropping land use[1] (by area) within upslope quadrant to 500 m	-	27	0.15	0.06	0.00	0.82
irrigcropppnUQ2000	proportion of irrigated cropping land use[1] (by area) within upslope quadrant to 2000 m	-	27	0.23	0.05	0.00	0.79
irrigcropppnUQ5000	proportion of irrigated cropping land use[1] (by area) within upslope quadrant to 5000 m	-	27	0.25	0.05	0.00	0.68
lippiacov	mean percent cover of lippia per site (1m x 1m quadrats; Ch.3)	%	27	16.46	2.99	0.63	74.00
meanGWalloc5000	mean groundwater allocation of licensed bores[3] within 5000 m buffer	-	27	387.22	34.62	134.80	707.67
north	northing[6]	-	27	6927541.93	3396.88	6899162.00	6975430.00
REarea500	area of mapped RE 11.3.25 or 11.3.4[2] within 500 m buffer	ha	27	23.20	3.33	1.81	62.54
REarea2000	area of mapped RE 11.3.25 or 11.3.4[2] within 2000 m buffer	ha	27	94.84	11.52	10.23	186.30
REarea5000	area of mapped RE 11.3.25 or 11.3.4[2] within 5000 m buffer	ha	27	254.75	21.94	49.98	385.26
REremppn500	proportion of mapped RE 11.3.25 or 11.3.4[2] remaining (proportion of preclear extent) within 500 m buffer	-	27	0.53	0.09	0.15	2.28
REremppn2000	proportion of mapped RE 11.3.25 or 11.3.4[2] remaining (proportion of preclear extent) within 2000 m buffer	-	27	0.22	0.03	0.07	0.58
REremppn5000	proportion of mapped RE 11.3.25 or 11.3.4[2] remaining (proportion of preclear extent) within 5000 m buffer	-	27	0.18	0.02	0.07	0.41
REremppnUQ500	proportion of mapped RE 11.3.25 or 11.3.4[2] remaining (proportion of preclear extent) within upslope quadrant to 500 m	-	27	0.22	0.05	0.00	0.95
REremppnUQ2000	proportion of mapped RE 11.3.25 or 11.3.4[2] remaining (proportion of preclear extent) within upslope quadrant to 2000 m	-	27	0.09	0.01	0.01	0.25
REremppnUQ5000	proportion of mapped RE 11.3.25 or 11.3.4[2] remaining (proportion of preclear extent) within upslope quadrant to 5000 m	-	27	0.03	0.00	0.00	0.08
remvegarea500	area of mapped remnant vegetation[2] within 500 m buffer	ha	27	29.48	3.48	7.60	76.10
remvegarea2000	area of mapped remnant vegetation[2] within 2000 m buffer	ha	27	142.59	14.18	50.78	327.43
remvegarea5000	area of mapped remnant vegetation[2] within 5000 m buffer	ha	27	575.54	55.24	256.19	1425.05
remvegppn500	proportion of mapped remnant vegetation[2] (by area) within 500 m buffer	-	27	0.375	0.044	0.097	0.969
remvegppn2000	proportion of mapped remnant vegetation[2] (by area) within 2000 m buffer	-	27	0.113	0.011	0.040	0.261
remvegppn5000	proportion of mapped remnant vegetation[2] (by area) within 5000 m buffer	-	27	0.073	0.007	0.033	0.181

Environmental variable	**Details**	**units**	**n**	**Mean**	**SE**	**Minimum**	**Maximum**
ringtankarea500	area of ring tank storages[4] within 500 m buffer	ha	27	2.24	0.92	0.00	17.96
ringtankarea2000	area of ring tank storages[4] within 2000 m buffer	ha	27	30.33	6.65	0.00	99.07
ringtankarea5000	area of ring tank storages[4] within 5000 m buffer	ha	27	132.27	20.16	0.00	321.81
ringtankareaUQ500	area of ring tank storage[4] within upslope quadrant to 500 m	ha	27	0.90	0.53	0.00	11.40
ringtankareaUQ2000	area of ring tank storage[4] within upslope quadrant to 2000 m	ha	27	6.66	2.94	0.00	66.45
ringtankareaUQ5000	area of ring tank storage[4] within upslope quadrant to 5000 m	ha	27	28.30	7.96	0.00	114.25
ringtanknumUQ500	number of ring tank storages[4] within upslope quadrant to 500 m	-	27	0.11	0.06	0.00	1.00
ringtanknumUQ2000	number of ring tank storages[4] within upslope quadrant to 2000 m	-	27	0.30	0.10	0.00	2.00
ringtanknumUQ5000	number of ring tank storages[4] within upslope quadrant to 5000 m	-	27	1.63	0.39	0.00	6.00
ripwidthcurrent	riparian width (RE 11.3.25 or 11.3.4)[2]	m	27	355.00	51.23	77.38	975.59
ripwidthpreclear	riparian width (RE 11.3.25 or 11.3.4) preclearing[2]	m	27	1974.26	224.85	305.01	6630.76
waterbodyarea500	area of mapped water bodies[4] within 500 m buffer	ha	27	2.04	0.83	0.00	14.71
waterbodyarea2000	area of mapped water bodies[4] within 2000 m buffer	ha	27	26.77	5.35	0.00	88.79
waterbodyarea5000	area of mapped water bodies[4] within 5000 m buffer	ha	27	105.97	12.65	7.12	247.50
WWI	dieback severity index (Ch.4)	-	27	327.78	16.79	175.00	475.00

Appendix E Mean cover data and functional classifications for species recorded at St Ruth Reserve

Species	**Life history**	**Life form**	**Clonality**	**Frequency**	**Mean cover (SE)**
Asperula conferta	perennial	forb	nonclonal	18	0.62 (0.22)
Boerhavia dominii	perennial	forb	nonclonal	3	0.02 (0.01)
Bothriochloa ewartiana	perennial	tussock grass	nonclonal	3	0.11 (0.08)
Bulbine bulbosa	perennial	forb	nonclonal	2	0.00 (0.00)
Carex inversa	perennial	sedge	clonal	13	0.85 (0.57)
Chenopodium sp.	perennial	chenopod shrub	nonclonal	1	0.00 (0.00)
Chloris divaricata	perennial	tussock grass	clonal	7	0.36 (0.17)
Chloris truncata	perennial	grass	clonal	2	0.00 (0.00)
*Conyza bonariensis**	annual	forb	nonclonal	17	0.30 (0.07)
Cullen tenax	perennial	forb	nonclonal	3	0.00 (0.00)
*Cyclospermum leptophyllum**	annual	forb	nonclonal	2	0.03 (0.03)
Cynodon dactylon	perennial	grass	clonal	47	5.51 (1.30)
Cyperus gracilis	perennial	sedge	nonclonal	6	0.09 (0.04)
Cyperus gunnii	perennial	sedge	clonal	45	0.45 (0.08)
Dichanthium sericeum	perennial	tussock grass	nonclonal	17	0.94 (0.57)
Dichelchne micrantha	perennial	tussock grass	nonclonal	1	0.00 (0.00)
Digitaria divaricatissima	perennial	tussock grass	nonclonal	3	0.03 (0.02)
Einadia nutans/polygonoides	perennial	chenopod shrub	nonclonal	49	8.23 (1.70)
Elymus multiflorus/scaber	perennial	tussock grass	nonclonal	32	2.44 (0.63)
Eragrostis tenellula	annual	grass	nonclonal	1	0.01 (0.01)
Eriochloa pseudoacrotricha	short-lived	tussock grass	nonclonal	12	0.95 (0.44)
Euchiton involucratus	perennial	forb	clonal	3	0.03 (0.02)
Eulalia aurea	perennial	grass	clonal	10	0.96 (0.49)
Eustrephus latifolius	perennial	vine	nonclonal	1	0.00 (0.00)
*Glandularia aristigera**	perennial	forb	clonal	22	2.20 (0.82)
Glycine tabacina	perennial	forb	clonal	7	0.05 (0.02)
*Lepidium africanum/bonariense**	annual	forb	nonclonal	10	0.49 (0.19)
Lomandra multiflora	perennial	rush	nonclonal	1	0.03 (0.03)
Marsilea sp.	perennial	fern	clonal	46	0.58 (0.09)
*Opuntia aurantiaca**	perennial	cactus	nonclonal	2	0.06 (0.04)
*Opuntia stricta**	perennial	cactus	nonclonal	1	0.01 (0.01)
Oxalis perennans	perennial	forb	clonal	44	0.50 (0.10)
Panicum decompositum	perennial	tussock grass	nonclonal	2	0.15 (0.13)
*Panicum gilvum**	annual	grass	nonclonal	1	0.04 (0.04)
Panicum laevinode	annual	tussock grass	nonclonal	1	0.35 (0.35)
Panicum queenslandicum	perennial	tussock grass	nonclonal	16	0.74 (0.32)
Paspalidium distans	perennial	tussock grass	nonclonal	51	11.37 (2.29)
Paspalidium gracile	perennial	tussock grass	nonclonal	2	0.15 (0.12)
*Phyla canescens**	perennial	forb	clonal	69	27.93 (3.43)
Portulaca oleracea	short-lived	forb	nonclonal	4	0.03 (0.02)
Rumex brownii	perennial	forb	nonclonal	1	0.00 (0.00)
Salsola tragus	short-lived	chenopod shrub	nonclonal	25	3.53 (0.86)
*Sonchus oleraceus**	annual	forb	nonclonal	2	0.06 (0.04)
*Urochloa panicoides**	annual	grass	clonal	2	0.06 (0.04)
Vittadinia pterochaeta/sulcata	annual	forb	nonclonal	5	0.03 (0.02)

* alien species

Appendix F Soil analysis results for shallow and deep soil samples from St Ruth Reserve

Measure	**units**	**n**	**Mean**	**SE**	**Minimum**	**Maximum**
Shallow soils						
Calcium	mg/kg	24	6237.50	260.21	4100.00	9400.00
Calcium: Magnesium	-	24	1.82	0.08	1.40	3.20
Cation Exchange	meq/100g	24	51.20	1.74	34.61	71.07
Chloride	mg/kg	24	49.17	3.39	27.00	93.00
Electrical conductivity	dS/m	24	0.16	0.01	0.08	0.27
Exchange Calcium	%	24	60.71	0.77	54.40	72.40
Exchange Magnesium	%	24	33.83	0.72	22.70	38.40
Exchange Potassium	%	24	4.83	0.11	3.90	5.70
Exchange Sodium	%	24	0.66	0.09	0.40	2.70
Exchangeable Calcium	meq/100g	24	31.19	1.29	20.43	47.06
Exchangeable Magnesium	meq/100g	24	17.22	0.59	12.41	24.17
Exchangeable Potassium	meq/100g	24	2.46	0.08	1.53	3.34
Exchangeable Sodium	meq/100g	24	0.33	0.05	0.16	1.41
Magnesium	mg/kg	24	2062.50	72.44	1500.00	2900.00
Moisture	%	23	6.79	0.20	4.40	8.10
Nitrate Nitrogen	mg/kg	24	9.46	1.07	2.00	24.00
Organic Carbon	%	24	3.58	0.18	2.30	5.70
pH	-	24	7.32	0.04	6.99	7.90
Phosphorus - Colwell	mg/kg	24	164.58	8.64	104.00	258.00
Potassium	mg/kg	24	957.50	32.82	600.00	1300.00
Sodium	mg/kg	24	76.33	11.02	36.00	320.00
Sulphur - KCl	mg/kg	24	12.90	0.89	6.10	20.60
Deep soils						
Moisture	%	8	5.99	0.35	4.40	7.00
Electrical Conductivity	dS/m	8	0.11	0.02	0.05	0.18
Nitrate Nitrogen	mg/kg	8	1.81	0.76	0.50	7.00
Organic Carbon	%	8	1.19	0.10	0.80	1.50
pH	-	8	7.71	0.13	7.23	8.34
Phosphorus - Colwell	mg/kg	8	86.38	14.85	31.00	137.00