Riparian seed banks

A potential tool for revegetation to support riparian management and restoration

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For Louis, Rob and mum

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ABSTRACT

This thesis research focuses on soil and sediment seed banks within riparian zones and their potential application for the regeneration of riparian vegetation to support river management or river restoration activities. The research was carried out in the lower Hunter Valley catchment in south eastern Australia, and addresses four main aims: 1) to detect spatial trends in seed bank species richness, abundance and composition within the riparian zone and 2) to identify drivers of seed bank variability; 3) to assess the potential contribution of the seed bank to riparian vegetation and geomorphic river recovery; and 4) present implications for the use of seed bank-based revegetation as a tool in river management and restoration. The research examines the traits of species detected in the seed bank in relation to geomorphology and sedimentology, and perhaps most innovatively, biogeomorphology – the study of reciprocal interactions between vegetation and geomorphology that drive the succession of both. Four studies investigate: 1) riparian seed bank stratification in relation to geomorphology; 2) relationships between seed bank spatial variability, geomorphology and sedimentology; 3) the potential role of riparian seed banks in supporting biogeomorphic succession and river recovery; and 4) seed bank composition in relation to riparian condition. Collectively the research findings contribute a framework for distinguishing between areas of potentially high and low seed bank species richness (and to some extent abundance) in any riparian system, based on simple field indicators including vegetation, sedimentology and geomorphology. The research emphasises the suitability of riparian seed banks to support the stabilisation of sediment through the regeneration of the pioneer species which were found to dominate the seed bank. Potential challenges for seed bank-based revegetation are raised, such as the increasing presence of exotic and terrestrial species with riparian degradation. The thesis highlights situations for which seed-bank based regeneration may be particularly useful, such as initiating channel contraction processes through sediment stabilisation and aiding the establishment of groundcover in highly degraded river reaches.

CERTIFICATE

This thesis comprises an original contribution that has not been submitted in any form, for a higher degree at any other university or institution.

In the Introduction to this thesis I have indicated the contribution of my fellow authors for the three published papers, and final paper to be submitted. Non-author contributions to this thesis are included in the acknowledgements section of each data chapter.

The source of all information used is presented in the reference section of each chapter and Appendix 6 details all sources for the trait data used in chapters three, four and five.

Jessica O'Donnell

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I am indebted to my supervisor Kirstie Fryirs for taking a chance on a plant person and guiding me through the field of fluvial geomorphology. Kirstie's feedback was always rapid and no-nonsense ('yuk!'). Her depth of knowledge and dedication to her field was an inspiration and I was consistently buoyed throughout my PhD candidature by her enthusiasm and encouragement.

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Last, but in no way least, this thesis would not have been possible without the emotional, financial and technical support provided by my brilliant partner Rob Duong. I hope to make it up to him some day.

Chapter 1

Introduction

INTRODUCTION

Riparian seed banks

The overarching aim of this thesis research is to improve our understanding of riparian seed banks and to investigate the extent to which seed bank-derived vegetation could be used to support river management and achieve river restoration goals. Riparian ecosystems are those influenced by bodies of water such as a lakes or rivers. This research specifically focuses on seed banks within the sediment of sand-bed river systems and their associated floodplain sediments and soils. The seed bank studied includes seeds, spores, buds and vegetative particles from which plants can readily regenerate given appropriate conditions - essentially the greater *propagule bank* (e.g. Poiani and Johnson 1989), but henceforth referred to as the seed bank for simplicity. Seed bank formation is a complex process in any ecosystem, determined by species-specific differences in seed production, seed persistence, and the timing of seed release from past and present vegetation assemblages (Roberts 1981, Thompson 1987, Thompson 2000, Hopfensperger 2007, Kehr et al. 2014). The incorporation of seeds into soils and sediment is then dependent on a large range of biotic and abiotic factors such as predation and disturbance (Chambers and MacMahon 1994, Pettit and Froend 2001). In river ecosystems, flowing water and fluvial processes add a high degree of spatial complexity to both seed inputs and seed bank formation, which is evident in the patch mosaic of different geomorphic units and their associated vegetation assemblages that characterise the riparian zone (Harris 1987, Nilsson et al. 1991, van Coller et al. 2000, Jansson et al. 2005, Richardson et al. 2007, Nilsson et al. 2010).

Prior to 2001, few studies had attempted to examine seed banks in riparian systems (Goodson et al. 2001). It was suggested that the paucity of research devoted to riparian seed banks at the time was due to the daunting task of unravelling the many factors influencing seed bank formation. Since then, a significant body of research has greatly expanded our understanding of riparian seed banks. For example, the composition of seed banks in floodplain, channel banks, bars and the channel bed have now been examined across a range of different riparian ecosystems (Brock and Rogers 1998, Abernethy and Willby 1999, Goodson et al. 2002, Middleton 2003, Capon and Brock 2006, Capon 2007, Gurnell et al. 2007). We know that riparian seed banks, like their terrestrial counterparts, are generally dominated by herbaceous species, and pioneer or early-successional species which are capable of establishing under adverse environmental conditions such as frequent disturbance or low nutrient availability (Bossuyt and Honnay 2008). As such, seed banks rarely show high similarity to established later-successional vegetation assemblages (Capon and Brock 2006, Hopfensperger 2007, Williams et al. 2008). We have a better understanding of the nature of seed inputs in the riparian zone and the importance of hydrochory for increasing seed bank species richness, and influencing the growth forms represented in the seed bank (Goodson et al. 2003, Jansson et al. 2005, Tabacchi et al. 2005, Gurnell et al. 2008, Moggridge et al. 2009). We also have a better understanding of the role of disturbances such as sediment deposition and erosion in determining seed bank characteristics and rates of seed bank turnover (Goodson et al. 2002, Gurnell et al. 2007).

So what can riparian land managers investigating seed bank-based revegetation draw from the current state of riparian seed bank knowledge? Most clear is the limitation

presented by the dominance of pioneer species in the seed bank (Bossuyt and Honnay 2008). However, currently no clear framework exists that riparian land managers can use to better understand the spatial variability of important seed bank characteristics such as abundance and species richness within their river reaches. For example, where in a river reach is the seed bank likely to be abundant, or particularly diverse? The first part of this thesis aims to contribute such a framework through the appraisal of the factors that influence seed bank formation and hence seed bank characteristics, in different locations within the riparian zone. To achieve this, comparisons are drawn between the seed banks of three different geomorphic units commonly associated with sand and gravel bed river systems: bars, benches and the floodplain. These units are described in detail in chapters two and four. The seed bank in each is examined with respect to the standing vegetation, hydrological conditions, and fluvial processes that influence both the formation of the unit, and the nature of seed inputs to the seed bank.

Riparian degradation and seed bank-based revegetation as a river management and restoration tool

The second part of this thesis aims to investigate how seed-bank based revegetation can be used as a tool to support river management and restoration. Land modification and the widespread clearing of vegetation in catchments and riparian zones have contributed to the degradation of many rivers (Booth and Jackson 1997, Foley et al. 2005, Richardson et al. 2007). Some significant issues include the erosion of hillslopes and river channels and corresponding oversupply of sediment (Wasson et al. 1998, Prosser et al. 2001), the delivery of agricultural runoff and eutrophication of waterways (Ulén et al. 2007), the loss or alteration of physical habitat for both aquatic

and terrestrial organisms (Pusey and Arthington 2003, Moore and Palmer 2005), and the encroachment of exotic and invasive plant species (Hood and Naiman 2000, Tabacchi et al. 2005). Vegetation provides a myriad of ecosystem services, and re-establishing vegetation on floodplains and within river channels may aid many aspects of river recovery (Abernethy and Rutherfurd 1998, Tabacchi et al. 1998, Abernethy and Rutherfurd 1999, Rutherfurd et al. 2000). Seed banks are recognised as one such source for the regeneration of vegetation (e.g. Brock and Rogers 1998, Middleton 2003, Bossuyt and Honnay 2008). However, there has been limited examination of the different ways seed-bank based revegetation may contribute to the management and restoration of rivers.

The role of the seed bank in riparian restoration is most commonly couched in terms of the potential contribution of the seed bank to regenerating floodplain vegetation (e.g. Brock and Rogers 1998, Pettit and Froend 2001, Robertson and James 2007, Boudell and Stromberg 2008, Greet et al. 2012). Studies tend to compare the seed bank to the standing vegetation with the aim of detecting differences between the two. For example, growth form representation (Pettit and Froend 2001, Middleton 2003, Bossuyt and Honnay 2008, Greet et al. 2012), exotic and/or native species richness (Williams et al. 2008, Greet et al. 2012), and plant strategies (e.g. habitat tolerances; Boudell and Stromberg 2008, Cui et al. 2013) are often compared. Other studies focus on the cause of differences between the seed bank and standing vegetation by comparing factors such as dispersal and seed persistence, and examining seed bank responses to different water regimes (Pettit and Froend 2001, Robertson and James 2007, Williams et al. 2008). Rarely is the potential *function* of the regenerating vegetation explored. For example, the growth of plants, from germinants to mature

individuals, can affect local hydrological conditions and fluvial processes (sediment erosion, transport and deposition) (Hupp and Osterkamp 1996, Erskine et al. 2009). The influence of a plant on these processes is determined by the traits of the plant in question. For example, we may compare the impact of herbs versus trees (e.g. Corenblit et al. 2007).

The second part of this thesis examines the potential role of seed bank-based regeneration in supporting the geomorphic recovery of degraded river reaches. Many rivers have suffered extensive erosion, incision and channel-widening due to the removal of vegetation in combination with the introduction of livestock grazing (Brooks and Brierley 1997, Prosser et al. 2001, Brierley et al. 2005, Fryirs et al. 2009). In many cases, it is recognised that re-establishing vegetation both on the floodplain and within the channel could help to arrest further erosion and initiate channel contraction processes (Abernethy and Rutherfurd 1998, Abernethy and Rutherfurd 1999, Rutherfurd et al. 2000). River reaches which have historically suffered extensive erosion can show signs of recovery in the form of channel contraction through the formation of vegetated bars and benches (the latter also referred to as 'active shelves') (Hupp 1992, Erskine 1996, Hupp and Osterkamp 1996, Brierley and Fryirs 2005, Erskine et al. 2009, Erskine and Chalmers 2009). This thesis investigates the potential role of the seed bank in initiating and/or supporting these particular natural recovery processes. Plant species traits are used to examine the influence of different assemblages of species regenerating from the seed bank on biogeomorphic processes (reciprocal interactions between plants, hydrology, fluvial processes and geomorphology; Corenblit et al. 2007). The findings of the research have implications

for the use of seed bank-based revegetation to achieve wider river management and restoration goals.

Study catchment: Wollombi Brook

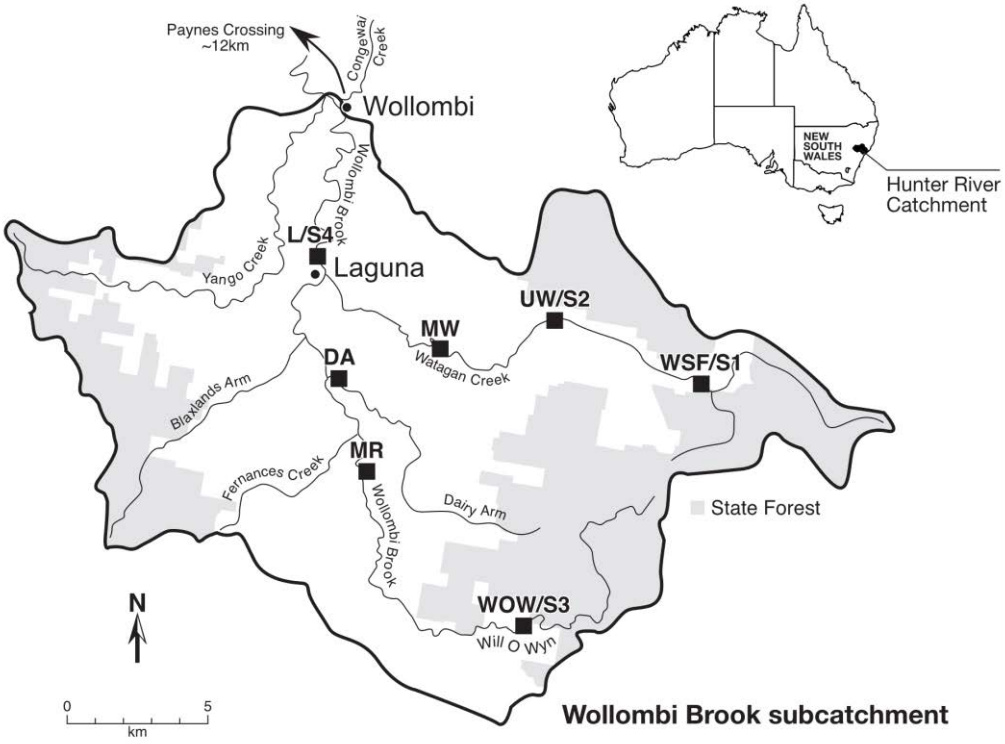
The research was carried out in Wollombi Brook, a subcatchment located in the southern part of the Hunter River catchment in south eastern Australia (Figure 1). A significant body of research relating to the pre- and post-European settlement flood history and related geomorphic and vegetation change has been conducted in this 341 km^2 catchment (Erskine 1994, Bennett and Mooney 2003, Erskine and Melville 2008, Erskine and Chalmers 2009, Jones and Byrne 2010, Fryirs et al. 2012). These publications provide detailed information on the regional setting, climate, geology and flood history of the catchment, and this information is outlined in the four data chapters of this thesis.

Most importantly, this catchment is representative of a trajectory of riparian degradation that is common in the New World (Prosser et al. 2001, Brierley et al. 2005). European settlement of the area commenced in 1823 and resulted in the widespread clearance of vegetation on the floodplain and along the river channels (Bloomfield 1954, Robinson 1959, Grady 1963, Parkes 1979). Extensive erosion and channel incision was initiated in the upper-mid-catchment reaches by a series of relatively small floods in 1927 and 1929, which resulted in the deposition of a large sediment slug in the mid reaches around Dairy Arm. A series of destructive floods in the 1940s initiated further erosion and transformed the mid channel reaches of Wollombi from a sinuous, vegetated small-capacity reach to a much wider and vegetation-free sand-dominated reach (Erskine 1994, Erskine and Peacock 2002).

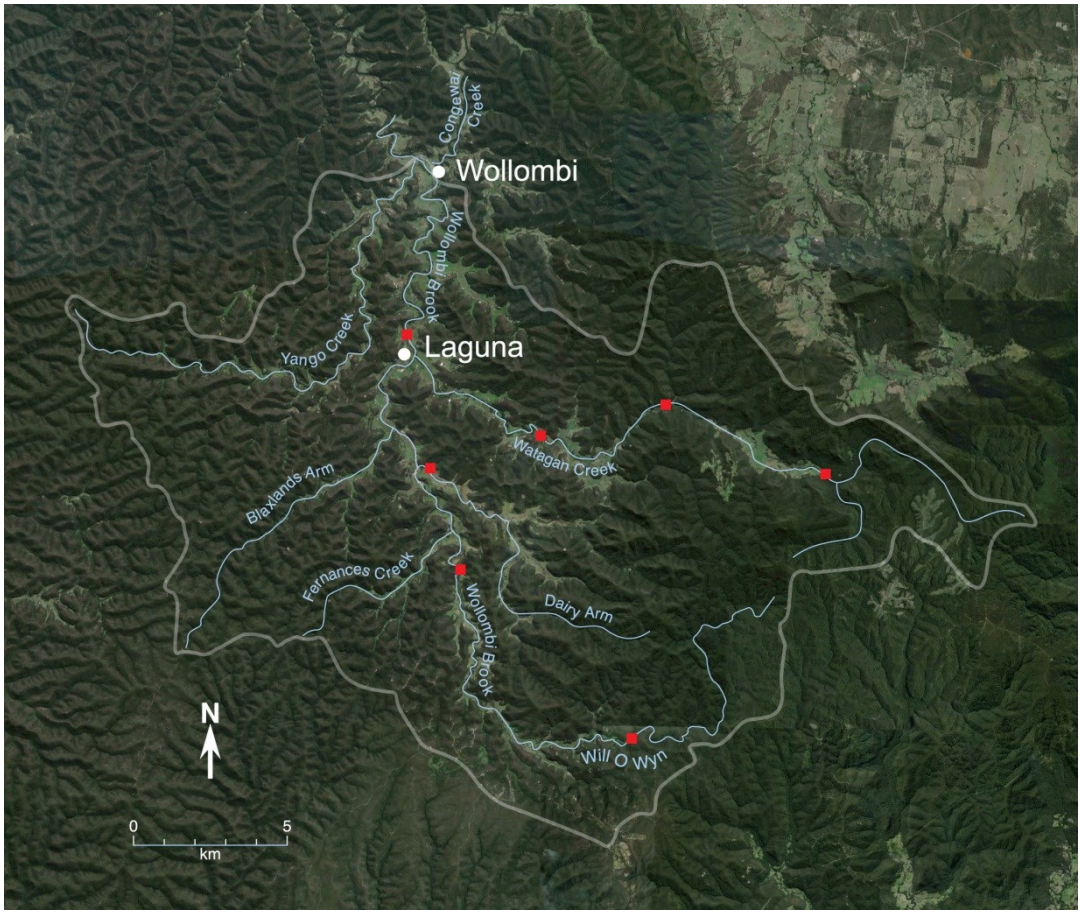
Much regeneration of vegetation has occurred on the hill slopes in the last fifty years as the extent of agriculture has declined, and deintensification of land use in the last twenty years has allowed the regeneration of vegetation along and within the river channels (Erskine and Chalmers 2009). The increasing development of vegetation within the channel has initiated channel contraction and prevented further erosion episodes in these recovering reaches, even during severe floods such as those which occurred in 2007 (Erskine and Chalmers 2009).

Figure 1 (opposite page) – a) Map of the Wollombi Brook subcatchment, including the location of the seven study reaches. Study reach names are presented as referred to in data chapters: study reaches Watagan State Forest (WSF/S1), Upper Watagan (UW/S2) and Mid Watagan (MW) are situated along Watagan Creek; study reaches Will O Wyn (WOW/S3), Murrays Run (MR), and Laguna (L/S4) are situated along Wollombi Brook; study reach at Dairy Arm (DA); b) Satellite image Wollombi Brook subcatchment (boundary indicated by grey line) including the seven study reaches (indicated in red). Dark green areas are forested hillslopes and light green areas the floodplain, which has been mostly cleared of vegetation.

a)


Paynes Crossing
~12km
Congewai Creek
Wollombi
Wollombi Brook
L/S4
Laguna
Yango Creek
UW/S2
MW
Watagan Creek
DA
WSF/S1
Blaxlands Arm
MR
Fernances Creek
Wollombi Brook
Dairy Arm
State Forest
N
WOW/S3
Will O Wyn
0
5
km
Wollombi Brook subcatchment
NEW SOUTH WALES
Hunter River Catchment

b)


Congewai Creek
Wollombi
Wollombi Brook
Laguna
Yango Creek
Watagan Creek
Blaxlands Arm
Fernances Creek
Wollombi Brook
Dairy Arm
N
Will O Wyn
0
5
km

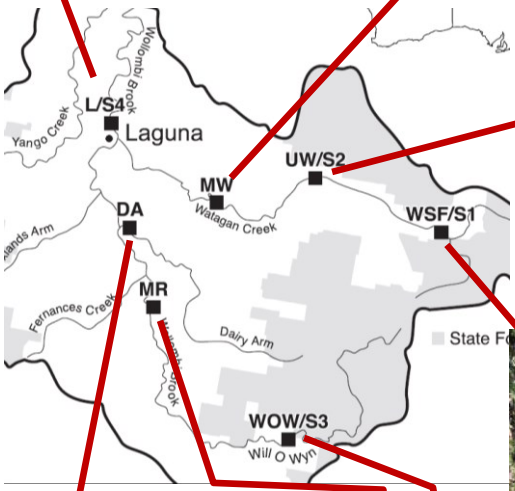
This research in this thesis examines the seed bank of seven study reaches in the Wollombi catchment (Figures 1a,b and Figure 2). It focuses on the seed bank of the floodplain, the channel bank and two within-channel geomorphic units: bars and benches. Bars and benches are common in sand and gravel bed river reaches and are important indicators of channel adjustment (Osterkamp and Hupp 1984, Hupp and Osterkamp 1996, Brierley and Fryirs 2005, Erskine et al. 2009). Examples of bars and benches in several of the study reaches are provided in Figure 3.

Figure 2 (opposite page) – Representative images of the seven study reaches in the Wollombi subcatchment.

Laguna (Wollombi Brook)

Mid Watagan Creek

Upper Watagan Creek



Watagan State Forest (Watagan Creek)

Dairy Arm

Will O Wyn
(Wollombi Brook)

Murrays Run (Wollombi Brook)

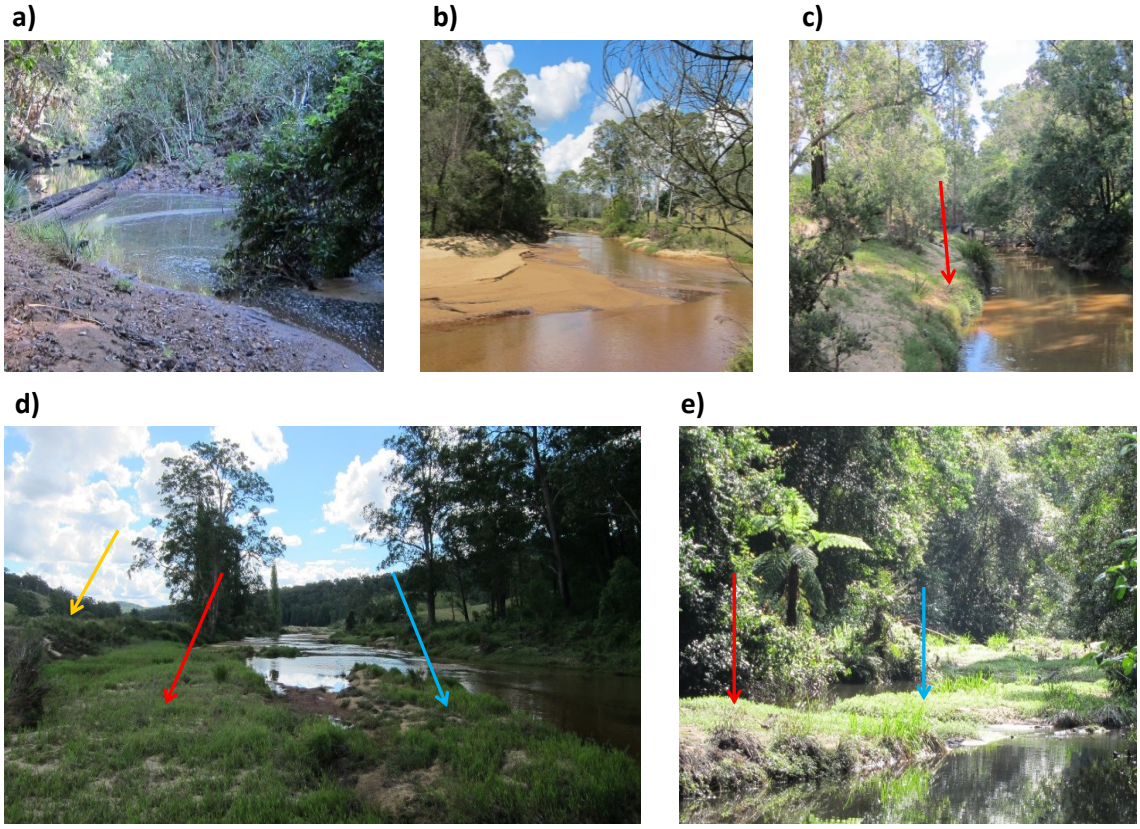


Figure 3 – Examples of bars and benches in the study reaches: a) bar in foreground on the Watagan State Forest reach of Watagan Creek (WSF/S1); b) bar at Dairy Arm (DA); c) bench along Laguna reach of Wollombi Brook (L/S4); d) vegetated bar (blue arrow) and bench (red arrow) on the sediment slug in the reach at Dairy Arm (DA). Yellow arrow indicates top of the channel bank and start of floodplain; e) vegetated bar (blue arrow) and bench (red arrow) along the Will O Wyn reach of Wollombi Brook (WOW/S3).

The seven reaches represent differing degrees of initial modification and degradation, and different stages of natural recovery from common issues such as erosion or the corresponding oversupply of sediment (c.f. Fryirs et al. 2009). Reaches WOW and WSF are valley-confined sand-bed reaches with occasional floodplain pockets and lie in the upper reaches of Wollombi Brook and Watagan Creek, respectively. These reaches contain intact vegetation and are significantly less modified than those of the lower catchment. Bench development is more obvious in WOW (Figure 3e), than WSF in

which bars are more common geomorphic units (e.g. Figure 3a). Reaches L, MW, MR and UW, are all partly-confined, planform-controlled, sand-bed reaches with discontinuous pockets of floodplain and represent varying degrees of recovery from historical erosion. All four reaches have well defined bars and benches. Large sections of the floodplain of L and MR reaches are devoid of overstorey vegetation and both lack a significant riparian vegetation strip. Exotic species dominate the local vegetation. In contrast, the floodplain vegetation and riparian strip in reaches MW and UW is more intact. While exotic species are present in these two reaches, they are less pervasive. Dairy Arm (DA) is partly-confined, planform-controlled, sand-bed river with discontinuous floodplain pockets, and is the most disturbed of the study reaches. This once sinuous and meandering reach has been significantly straightened and over-widened as a result of historical erosion (Fryirs et al. 2012). The channel and floodplain contain an extensive sediment slug and sandy 'floodout', respectively, derived from the erosion that occurred in the mid reaches of the catchment during the floods of the 1920s and 1940s (Erskine 1994, Erskine and Melville 2008). The development of sand bars and wide, vegetated benches that are tending toward inset floodplain are indicative of gradual recovery (Figure 3d).

Thesis aims, scope and structure

This thesis has four specific aims:

Aim 1: *To detect spatial trends in seed bank species richness, abundance and composition, within the riparian zone.*

Aim 2: *To investigate the drivers of observed seed bank characteristics and their spatial variability.*

Aim 3: *To assess the potential contribution of seed bank-based regeneration to riparian vegetation and geomorphic river recovery.*

Aim 4: *To present implications for the use of seed bank-based revegetation as a tool in river management and recovery*

This thesis consists of six chapters – this Introduction, four data chapters, and a final discussion section which provides a synthesis of the research findings in relation to the aims of the thesis, and the relevance and contribution of the research findings to international riparian seed bank research. Supplementary material relating to the data chapters is provided in six appendices.

All data chapters are reproduced directly from the journals in which they were published. As such, the reader will note differences in formatting, referencing styles and section headings. The reader will also note some unavoidable repetition of introductory material including information regarding the nature of seed banks, the study catchment and experimental methods, which was required for inclusion in each individual manuscript.

The four data chapters present a sequence of investigation that moves from study of spatial variability in riparian seed banks and the potential drivers of that variability (chapters two and three), to an examination the role of the seed bank-based regeneration in biogeomorphic succession and geomorphic river recovery (chapter four). Chapter five examines how riparian condition influences the utility of the seed bank for geomorphic and ecological river recovery.

A brief summary of each data chapter and a breakdown of the contribution of each author (Jessica O'Donnell [JOD], Kirstie Fryirs [KF] and Michelle Leishman [ML]) to each manuscript are presented below.

Chapter 2 – Riparian seed bank stratification

This chapter, published in *Freshwater Biology* under the title *'Digging deep for diversity: riparian seed bank abundance and species richness in relation to burial depth'*, examines seed bank stratification within three discreet depositional geomorphic units: bars, benches and floodplain along four study reaches. A seedling emergence glasshouse study (seedling emergence study no. 1 – Appendix 4) is used to characterise seed bank abundance and species richness in 5 cm intervals to a depth of 30 cm in each unit. Bar and bench seed bank characteristics are found to be variable with depth, while floodplain seed abundance and species richness decline with depth. Bars display the highest variability in seed bank abundance, and significantly lower species richness than benches and the floodplain. Seed bank stratification differences between the units are considered to relate to their relative differences in inundation and disturbance frequencies. Inundation frequency influences the vertical formation of seed banks along with the geomorphic unit, and the capacity for seeds to be removed from sediments. This research was carried out at study reaches WOW, WSF, MW and L, which were chosen as moderate to good condition sites, representative of the mid and upper reaches of the catchment.

Field work – Carried out by JOD and KF
Glasshouse and Lab work – Carried out by JOD
Data compilation and analysis – Compiled and analysed by JOD. ML provided assistance on statistical approach.

Writing – JOD developed the manuscript including body of text, tables and figures, which were subsequently edited by KF and ML. KF contributed some text to the methods in relation to the study sites and catchment. JOD prepared manuscript for submission.

Intellectual contribution – JOD provided the bulk of the intellectual contribution. KF provided input on fluvial geomorphological concepts.

Chapter 3 – Riparian seed banks and sedimentology

Chapter three, published in *Geomorphology* under the title '*Can the morphological and sedimentological structure of rivers be used to predict characteristics of riparian seed banks?*' attempts to measure the extent to which seed bank characteristics (abundance, species richness, average seed mass and average seed shape) of bars, benches and the floodplain are correlated with sedimentological factors related to particle size and organic matter content. The research utilises data from seedling emergence study no. 1 (Appendix 4), and additional sedimentological analyses. Seed bank abundance and species richness are found to be weakly but significantly positively related to increasing percentage of fine particles and decreasing percentage of sand/gravel particles, and species richness is positively related to increasing sediment organic matter content and decreasing median sediment particle size. No relationship is found between seed characteristics and sedimentology. A framework is presented that outlines how geomorphology and hydrology ultimately drive spatial variability in seed bank characteristics by (1) directly influencing seed inputs and losses from seed banks via erosion and deposition (fluvial processes) and (2) indirectly influencing seed inputs and losses by mediating seed germination and mortality and the establishment success of plants. The capacity for geomorphic units, related vegetation and sedimentological qualities to be used as indicators of the dominant

processes influencing seed bank characteristics within the riparian zone is highlighted. This research was carried out at study reaches WOW, WSF, MW and L, which were chosen as moderate to good condition sites, representative of the mid and upper reaches of the catchment.

Field work – Carried out by JOD and KF
Glasshouse and Lab work – Carried out by JOD
Data compilation and analysis – Compiled and analysed by JOD.
Writing – JOD developed the manuscript including body of text, tables and figures, which were subsequently edited by KF and ML. JOD prepared manuscript for submission.
Intellectual contribution – JOD provided the bulk of the intellectual contribution. KF provided input on fluvial geomorphological concepts, sedimentological analyses and regional setting. ML directed the statistical approach.

Chapter 4 – Riparian seed banks and biogeomorphic succession

Chapter four, published in *River Research and Applications* under the title '*Can the regeneration of vegetation from riparian seed banks support biogeomorphic succession and the geomorphic recovery of degraded river channels?*' assesses the capacity of the seed bank to contribute to three different stages of biogeomorphic succession represented by bars, benches and the floodplain, and their associated vegetation. The research utilises the data from seedling emergence study no. 1 (Appendix 4), the results of the vegetation survey (Appendix 6), and plant trait data (Appendix 3). The seed bank and standing vegetation associated with each unit is analysed in relation to species richness and composition, and three plant species traits - plant longevity, growth form and seed dispersal mechanism. Bar, bench and floodplain seed banks are found to be compositionally similar to the vegetation associated with bars - mostly

perennial pioneer herbs, sedges and rushes that are dispersed by wind and hydrochory (water transport). The results highlight the potential utility of the seed bank in supporting early stages of biogeomorphic succession, which is essential for initiating channel contraction processes in degraded river reaches. This research was carried out at study reaches WOW, WSF, MW and L, which were chosen as moderate to good condition sites, representative of the mid and upper reaches of the catchment.

Field work – Carried out by JOD and KF
Glasshouse and Lab work – Carried out by JOD
Data compilation and analysis – Compiled and analysed by JOD.
Writing – JOD developed manuscript including body of text, tables and figures, which were subsequently edited by KF and ML. JOD prepared manuscript for submission.
Intellectual contribution – JOD provided the bulk of the intellectual contribution. KF provided input on fluvial geomorphological concepts. ML provided input on statistical approach.

Chapter 5 – Seed banks, riparian condition and restoration

This chapter, published in *Science of the Total Environment* under the title '*Seed banks as a source of vegetation regeneration to support the recovery of degraded rivers: a comparison of river reaches of varying condition*', builds upon the findings in chapter four. It explores how the capacity for seed bank-based regeneration to contribute to geomorphic river recovery (without compromising other ecological restoration goals) is affected by riparian condition. Plant growth forms comprising the native and exotic component of the seed bank and standing vegetation are compared between seven river reaches assessed as being in poor (one reach), moderate (four reaches) and good condition (two reaches). Native species richness in the seed bank is found to be comparable across all condition reaches and pioneer species dominant. However, the

propagules of exotic species (considered an impediment to achieving ecological restoration goals), increasingly dominate the seed bank as condition deteriorates. The seed bank also reflects the increasing dominance of terrestrial exotic species over native riparian species in the standing vegetation, which is associated with riparian degradation. Considering the resources required to control the regeneration of the exotic species that germinate from the seed bank, the application of seed-bank based regeneration in poor condition reaches, with little follow up management may provide the greatest contribution to river recovery for the effort expended. The research utlises the results of seedling emergence experiment no. 2 (Appendix 5) and the vegetation survey (Appendix 6). This research involved all seven study sites, which together were representative of poor (reach L), moderate (reaches L, MR, MW, UW) and good condition reaches (WOW, WSF) within the catchment.

Field work – Carried out by JOD
Glasshouse and Lab work – Carried out by JOD
Data compilation and analysis – Compiled and analysed by JOD.
Writing – JOD developed manuscript including body of text, tables and figures, which were subsequently edited by KF and ML. KF contributed material relating to the geomorphic assessment of river condition. KF also provided information on Wollombi catchment and the catchment flood history which was modified by JOD. JOD prepared manuscripts for submission.
Intellectual contribution – JOD primarily developed the research approach, KF contributed concepts related to geomorphic river condition assessment and river management and ML provided input on ecological condition assessment approaches. JOD, KF and ML all had input into interpreting the research findings.

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Chapter 2

Riparian seed bank stratification

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Digging deep for diversity: riparian seed bank abundance and species richness in relation to burial depth

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SUMMARY

1. Soil and sediment seed banks contribute to the diversity of riparian plant communities. In degraded river systems, seed banks represent an important regeneration niche that may contribute to restoration efforts through the establishment of vegetation. The vertical dimension of seed banks has been neglected in river research, despite its importance for the regeneration of vegetation after disturbances such as erosive floods.
2. We sampled sediment at various depths within three geomorphological features: bars, benches and the floodplain, across four river reaches in the Wollombi subcatchment of New South Wales, Australia. A seedling emergence study was conducted to characterise the abundance and species richness of the germinable seed bank within these sediments. We hypothesised that the vertical distribution of seeds in bars and benches would show no clear pattern, but that bars would have lower propagule counts overall, due to their non-cohesive sediment and potential for frequent reworking by low-level flows. The floodplain seed bank, in contrast, would resemble that of terrestrial systems, with propagule abundance decreasing markedly with depth due to infrequent inundation and sediment reworking.
3. In total, 9456 seedlings emerged, representing 131 different species (83 native and 47 exotic) from 47 families. Propagule abundance and species richness in bar and bench seed banks were highly variable with depth, with the greatest average propagule numbers found at 25–30 cm and 20–25 cm, respectively. In contrast, and as hypothesised, propagule abundance and species richness in the floodplain decreased significantly with depth. Propagule abundance was surprisingly variable in bars, with some displaying extremely high values and others containing no detectable seeds, although overall species richness was significantly lower than in benches and the floodplain.
4. The vertical distribution of seeds in bars, benches and floodplains may be determined by the proportional influence of hydrochory (seed transport and deposition by water) during deposition events and seed losses, resulting from sediment reworking and erosion, set within the timescales over which they are formed and reworked. Bar seed banks are continually flushed by frequent inundation and reworking, especially at the surface, reducing seed deposition and burial. Abundant seed fall may be provided by local vegetation, however. Diverse seed banks in benches may form through alternating periods of hydrochoric seed deposition along with sediment, augmented during periods of exposure when propagules from the extant vegetation accumulate. Decreases in germinable propagule abundance and species richness with depth in the floodplain may reflect much slower rates of vertical accretion and seed losses due to mortality over time. Finally, we present some implications for the management of riparian vegetation and applications for river restoration.

Keywords: propagule, geomorphic unit, riparian, seed bank, vertical stratification

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Introduction

Seed banks are a fundamentally important component of plant communities (Warr, Thompson & Kent, 1993). At the species level, seed banks act as an ecological 'bet-hedging' strategy, providing many opportunities for germination and, as such, can contribute to species coexistence and diversity (Thompson, 2000). At the community level, seed banks increase the resilience of plant communities to physical disturbance by allowing rapid regeneration (Roberts, 1981; Poiani & Johnson, 1989). Use or manipulation of soil seed banks in the rehabilitation of vegetation is common at mining sites (Roche, Koch & Dixon, 1997; Zhang *et al.*, 2001), although there is the potential for its application in a wide array of landscapes, from wetlands to forests (Putwain & Gillham, 1990; Clevering, 1995; Augusto *et al.*, 2001; Jensen, Walker & Paton, 2008).

Germinable seed banks in terrestrial environments are often concentrated near the soil surface and are assumed to decrease linearly with soil depth (Bekker *et al.*, 1998; Traba, Azcárate & Peco, 2004). As such, standard sampling procedures rarely extend beyond depths of 10 cm. In disturbed environments, however, where soil reworking is more frequent, it is likely that a) viable seeds will occur at much greater depths (e.g. see examples in Major & Pyott, 1966) and b) deeply buried seeds may be more frequently brought to the surface and exposed to light and temperatures conducive to germination and establishment (Bliss & Smith, 1985; Benvenuti, Macchia & Miele, 2001).

River ecosystems are dynamic environments, within which seed inputs and losses influence the formation of riparian seed banks. Riparian seed banks are derived from a variety of sources, including seed rain from the surrounding environment and hydrochory (the transport and deposition of seeds by water). Hydrochory delivers propagules (seeds, spores and vegetative fragments) from upstream vegetation in conjunction with waterborne sediment during inundation events that result in deposition (Chambert & James, 2009). Ultimately, this sediment–seed mix forms the seed bank within different geomorphological structures, or *geomorphic units* (*sensu* Brierley & Fryirs, 2005), such as bars, benches and floodplains, that are formed under flows of varying magnitude (Wolman & Gerson, 1978). During periods of geomorphological stability between disturbance events (i.e. flows that induce erosion or deposition), additional propagules will accumulate on the surface of these units from surrounding vegetation via seed rain and dispersal agents such as wind and animals. Over time, some seeds will be lost permanently from the seed bank through germination, predation and mortality (Grillas *et al.*, 1993; Bonis & Lepart, 1994). Other seeds may be redistributed within the seed bank or be completely remobilised when the sediment is reworked by flows. As such, the vertical profile of the seed bank in any geomorphic unit will partly depend on the historical pattern of erosion and deposition for that unit. In their review of riparian seed banks, Goodson *et al.* (2001) highlight the lack of knowledge about the number and types of propagules housed within different geomorphic unit types, and how the composition and abundance of propagules deeper within the sediment profile may affect the reestablishment of vegetation after erosion events.

The composition and abundance of riparian seed banks have been studied in a range of fluvial landforms. For example, Gurnell *et al.* (2007a) found a continually changing mix of propagules within the channel bed. In contrast, the faces of eroding banks of the River Dove in the United Kingdom were found to house considerably fewer propagules than the bank top and toe (Goodson *et al.*, 2002), while floodplain seed banks often contain diverse and abundant seed banks dominated by annual species (Capon & Brock, 2006; Webb *et al.*, 2006; Jensen *et al.*, 2008). The deposition of seeds via hydrochory is strongly influenced by channel morphology, hydrology and roughness (vegetation and wood) (Goodson *et al.*, 2002; Gurnell *et al.*, 2006a,b; Pettit & Naiman, 2006; Engstrom, Nilsson & Jansson, 2009). Few studies have considered the vertical dimension of seed banks in these highly dynamic systems, although evidence of compositional changes in seed species has been found in depths as little as 10 cm (Boudell & Stromberg, 2008a). Understanding seed bank diversity and abundance in deeper layers of soil and sediment will provide a clearer estimate of the potential for seed banks in different geomorphic units to contribute to vegetation dynamics within riparian systems (Goodson *et al.*, 2001), while substantial compositional diversity may be missed by sampling only at the surface.

Deeply buried seeds have an important role to play in determining community resilience and can potentially aid restoration. For example, sand and gravel bed rivers in Australia have been subjected to severe erosion as a result of anthropogenic activity such as vegetation clearing and removal of wood (Erskine & Saynor, 1996; Brooks & Brierley, 1997; Fryirs, Brierley & Erskine, 2012). However, a diverse array of depositional fluvial landforms, or geomorphic units, such as bars and benches indicates recent readjustment and channel contraction processes in these systems. The establishment of vegetation to 'stabilise' these features, particularly after

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erosion events, is often a key component of river rehabilitation, and initial germination and seedling establishment are often provided by the seed bank (Erskine & Livingstone, 1999; Thompson, 2000; Fryirs, Spink & Brierley, 2009). However, to what depths can we rely on this seed supply for regeneration? For land managers, greater understanding of the vertical extent and composition of riparian seed banks will provide an indication of the capacity for the re-establishment of vegetation following disturbances (Fryirs & Brierley, 2000; Williams *et al.*, 2008).

Our aim was to quantify the abundance and species richness of the seed bank in a riparian river system in relation to geomorphic unit type (bars, benches and floodplains) and depth. Each of these units has discrete surfaces, defined by a specific range of inundation, deposition and reworking dynamics (Fig. 1) (Fryirs & Brierley, 2013). For example, bars are frequently reworked and inundated and are comprised of non-cohesive sands. Benches are step-shaped features attached to the channel bank (Fryirs & Brierley, 2013) that sit higher than bars and are inundated and reworked with an intermediate frequency of in-channel flows. Benches are often vegetated and thus more cohesive and stable (Erskine & Livingstone, 1999). In contrast, the floodplain forms relatively flat surfaces outside the channel zone. These surfaces are infrequently inundated, and even less frequently reworked, during overbank flows. As such, the floodplain receives minimal seed input via hydrochory, with the majority of seed input from established floodplain vegetation.

Specifically we hypothesised that:

1) Seed bank abundance and species richness should show no clear pattern throughout the sediment profile in bars and benches, due to frequent and moderate inundation, and sediment reworking, respectively.

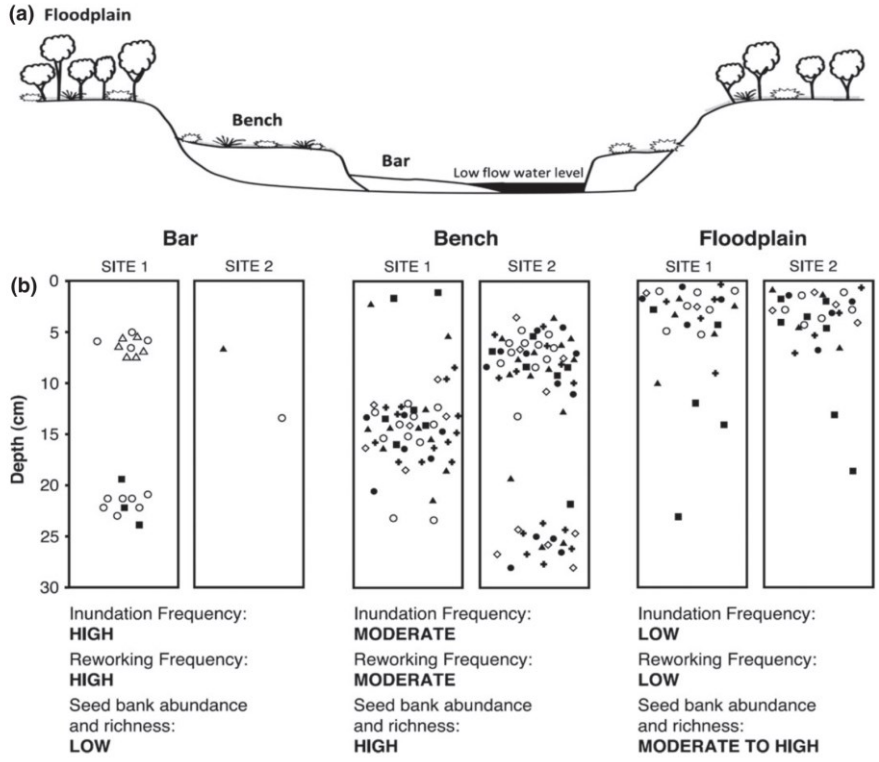

Fig. 1 (a) Diagram of a hypothetical river channel containing the three geomorphic unit types in this study: bars, benches and the floodplain. (b) Predicted patterns of abundance and species richness of the germinable seed bank with depth in bars, benches and the floodplain, each of which are characterised by differing disturbance (inundation and reworking) frequencies. Propagules of different species are represented by different shapes. Expected soil and sediment profiles for each geomorphic unit type are presented for two hypothetical sites to show the expected degree of variability between individual units of the same type within or between sites.

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2) Seed bank abundance and species richness would be lower in bars than in benches or floodplains, due to the position of bars and their potential for frequent reworking by low flows.

3) Seed bank abundance and species richness in floodplains should show a marked decline with depth due to infrequent inundation and sediment reworking (Fig. 1).

Methods

Study sites

We selected four stream reaches within the Wollombi Brook subcatchment of the Lower Hunter River catchment in New South Wales, Australia: two along Wollombi Brook, which drains a 341 km^2 basin at Laguna, and two along Watagan Creek, which is a major tributary of Wollombi Brook (Fig. 2). Both rivers are sand-dominated, derived from the Triassic intercalated sandstone and shale that comprises the catchment. Flood variability for Wollombi Brook is high by world standards and characterised by long periods of low flow (Erskine, 1996). Sites 1 and 2 were located in the upstream and middle reaches of Watagan Creek, respectively, while Sites 3 and 4 were in the upstream and middle reaches of Wollombi Brook, respectively (Fig. 2). All sites are well vegetated with both native and exotic species, although less encroachment by exotic species has occurred in the two upstream sites than in the middle reaches.

Study design

The four study reaches were chosen because they are largely undisturbed by human activity and are well vegetated, possessing at least three discrete examples of bars, benches and floodplains. Bars were defined as non-cohesive deposits of medium to coarse sand that are primarily bank-attached lateral bars or point bars (Brierley & Fryirs, 2005). They sit above the low flow water level between 5 and 60 cm. Benches were akin to the 'low' and 'middle' benches as described by Woodyer (1968), being generally flat topped bank-attached depositional structures topped with fine and medium sand. The degree of established vegetation on benches varied markedly both within and between sites. Generally, benches ranged between 60 cm and 1.8 m above the low flow water level. The extent of floodplain available for seed bank sampling varied between sites, and the height

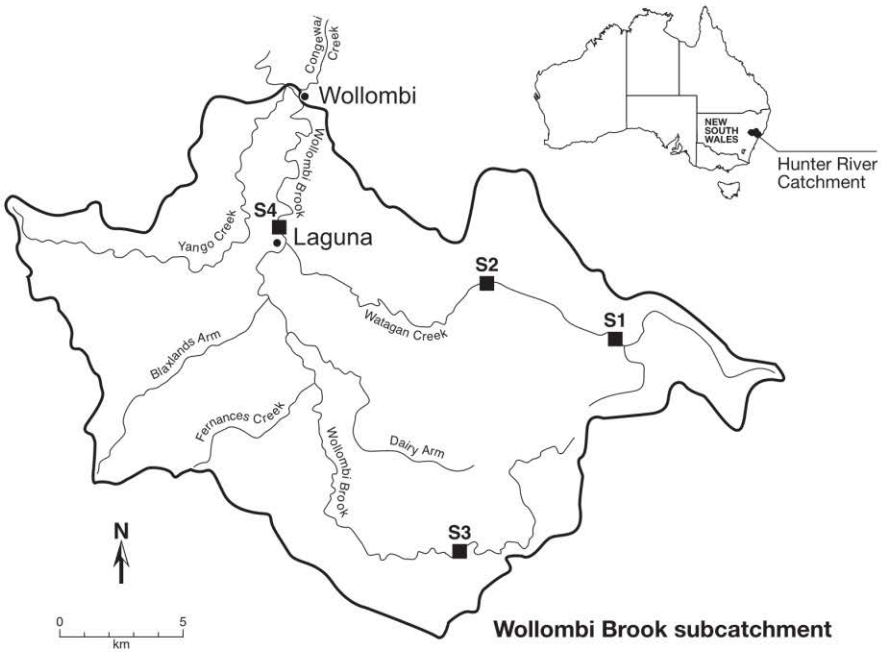

Fig. 2 Map showing the location of the four study sites situated along reaches of Wollombi Brook and Watagan Creek in the Wollombi Brook subcatchment of the lower Hunter River catchment of New South Wales, Australia. Map modified from Erskine & Melville (2008).

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of the floodplain above the low flow water level ranged between 3 m at Site 2 and 5 m at Site 3.

Soil and sediment sampling

At each of the four study reaches, three discrete bars and benches were identified and selected for sediment sampling. For the floodplain, three soil sampling locations were randomly selected within an area 0.5 m to 7 m from the top of the bank and along a 60 m length of the reach. All soil and sediment sampling were undertaken between late May and early August 2011. To extract the sediment from each unit, either two cores or one pit was excavated. At each 5-cm-depth interval, four subsamples of soil (floodplain) or sediment (bars and benches), each ranging between 200 and 300 cm^3, were removed from the sides of the pit or holes using a trowel. These were pooled in a single bag and thoroughly mixed. This process was repeated to a depth of 30 cm, resulting in six depth samples: 0–5, 5–10, 10–15, 15–20, 20–25 and 25–30 cm for each geomorphic unit replicate. In the case of several bars, sediment was sampled only to a depth of 20 cm, due to water infiltration and collapse of the pits that prevented the removal of sediment. A total of 203 samples were collected. The samples were refrigerated at 4 °C until the seedling emergence study began 2–12 days later.

Study of seedling emergence

A seedling emergence study was conducted in the Macquarie University glasshouse facility. From each pooled sample, 450 cm^3 of sediment was spread evenly over Greenlife™ commercially available washed river sand to a depth of approximately 1 cm, across four 12.5 cm × 7 cm seedling punnets, which were placed in one-half of a seedling tray. Six control trays were filled with washed river sand only, to confirm the absence of seeds. The seedling trays, each containing eight punnets holding two different samples, were distributed randomly within the glasshouse and redistributed randomly every month to reduce the effect of any spatial variation in environmental conditions within the glasshouse. The soil and sediment samples were moistened by mist watering for 1 to 2 min three to four times daily, depending on weather conditions. Glasshouse temperature ranged between 18 and 25 °C. After approximately 6 weeks, a small amount of Brunning's™ Nitrophoska Slow Release fertiliser for native plants was added to each punnet, to reduce the effects of nutrient leaching. The temperature, watering and fertilisation regimes were applied to promote maximum germination across as many species as possible.

Seedling emergence was monitored every 2 - 3 days. Each seedling was grown until it could be identified to species or replanted in pots and grown until flowering to aid identification. All species names conform to those recognised by the National Herbarium of New South Wales, Australia. For each species identified, data on growth form (tree, shrub, herb, grass, sedge, rush, fern), longevity (annual, biennial, perennial) and origin (native, exotic) were recorded using the PlantNET database (Botanic Gardens Trust, 2012).

Fern seedlings that germinated from spores, or seedlings that regenerated from stem and root fragments, were included in the study as well as seedlings that germinated from seeds. We refer to all these as the 'germinable seed bank' for ease of description. The term 'germinable' is used as the emergence method will not detect seeds or other propagules that are present yet fail to germinate due to either dormancy, or the absence of specific germination cues that were not provided in the glasshouse. For example, the watering regime employed partly determines the seeds that germinate (Poiani & Carter Johnson, 1988; Gurnell *et al.*, 2007b). Considering this, our results indicate which species within the seed bank will readily germinate and provide, at the very least, a conservative estimate of the true seed bank. The study continued until January 2012, by which time no new seedlings had been observed in any of the samples for at least 2 weeks.

Data analysis

Total seedling abundance and species richness data were collated for all soil and sediment samples. The seed abundance data were right-skewed and so were normalised with a $\log_{10}$ transformation which removed nine samples with zero counts, leaving 193 samples for further analysis.

To assess overall differences in the abundance and species richness of the germinable seed bank between sites, geomorphic unit and depth, we constructed a generalised linear mixed model (GLMM), based on a normal distribution with identity link function in SPSS, v. 20 (SPSS Inc, 2011). This model used Satterthwaite approximation for the degrees of freedom and robust estimation for the tests of the fixed effects, and their interaction was selected, as recommended for unbalanced datasets with complex covariances. Geomorphic unit type and sample depth were treated as fixed factors and site as a random factor. Restricted maximum likelihood (REML) was used to estimate the model parame-

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ters. The effect of depth on the germinable seed bank was also analysed for bars, benches and the floodplain separately, using the same procedure, except we did not assume robust covariances in these cases.

Analysis of the species richness data required several approaches. A square root transformation improved the normality of the data, although some deviation from the normal distribution remained (Kolmogorov–Smirnov test: D = 0.089, P = 0.001, Shapiro–Wilk test: W = 0.984, P = 0.023). Consequently, all analyses were conducted assuming a normal distribution and results interpreted cautiously. A GLMM was constructed incorporating the same fixed and random factors (geomorphic unit type and sample depth, and site, respectively), as used with the abundance data, to compare patterns of species richness with depth in bars, benches and the floodplain. Cumulative species richness with depth was investigated graphically to compare overall species richness within units with increasing depth and to account for different mixes of species at different depths. To achieve this, the species richness of the seed bank for the 0 - 5 cm sample was counted for each geomorphic unit replicate, and the number of new species encountered with each successive depth is presented.

Results

A total of 9456 seedlings emerged from the sediment and soil samples, representing 131 species and 47 families. The majority of seedlings germinated from seed, although several species, including *Axonopus fissifolius*, *Microlaena stipoides*, *Pratia purpurascens* and *Tradescantia fluminensis,* clearly generated from stem or root fragments. Five seedlings could be identified only to genus. The most common families were the grasses (Poaceae, 19 species), Asteraceae (15 species), sedges (Cyperaceae, 15 species) and rushes (Juncaceae, 13 species). Eighty-three of the species identified in the germinable seed bank were native and 47 were exotic, and, of 9454 propagules identified, 7944 (84%) were native and 1510 (16%) exotic. The species included a range of growth forms including herbs (56), sedges and rushes (32), grasses (15), shrubs and trees (13), ferns (8) vines/climbers (5) and aquatic herbs (2). Most species were also perennial (65%), although annuals and short-lived perennials made up 22% and 13% of the seed banks, respectively. A complete list of all species identified within the seed bank across all samples, including information on their native or exotic origin, growth form and longevity (annual/perennial), is provided in Supporting Information (Table S1).

Seed bank abundance and diversity in relation to depth

Patterns of the abundance of germinable seed with depth differed between the three geomorphic unit types (Figs 3 & 4a), and results of the GLMM showed a significant depth and unit type interaction ($F_{3,175}$ = 11.124, P = <0.001). When bars, benches and the floodplain were analysed separately, the abundance of germinable seeds in both bars and benches was highly variable between replicates, both within and across the four sites, such that no significant pattern with depth was evident. In contrast, and in support of our hypothesis, the germinable seed bank of the floodplain showed a significant pattern of decreasing abundance with depth (GLMM: $F_{5,63}$ = 5.439, P = <0.001). Unexpectedly, however, there were still surprisingly high numbers of viable propagules in even the deepest of the floodplain samples (Fig. 4a).

Patterns of species richness with depth in the germinable seed bank mirrored patterns of propagule abundance across all three units. Results of the GLMM showed a significant depth and unit type interaction ($F_{3,176}$ = 16.055, P = <0.001). Species richness in bars and benches was highly variable with depth (Fig. 4b) with the greatest species richness in the deepest samples at 25–30 cm and 20–25 cm in bars and benches, respectively. Again only the floodplain showed a significant pattern, with species richness of the germinable seed bank declining with depth (GLMM: $F_{5,63}$ = 6.939, P = <0.001) (Fig. 4b).

Seed bank abundance and diversity in relation to geomorphic unit

As mentioned above, results of the GLMM revealed a significant interaction between unit and depth, although there was no significant difference in the mean abundance of propagules between the total germinable seed bank (i.e. all depths combined) of bars (mean 427.83, SD = 645.28), benches (mean 166.58, SD = 125.45) and the floodplain (mean 193.67, SD = 92.95). On average, bars contained the most propagules, although this was highly variable between units (Fig. 5a). Species richness varied significantly between geomorphic units, and, as hypothesised, bars contained significantly fewer species (mean 12.92, SD = 6.47) than benches (mean 22.42, SD = 7.82) and the floodplain (mean 25.25, SD = 8.92) (GLMM: $F_{2,33}$ = 8.221, P = 0.001) (Fig. 5b).

There were significant reach/site differences in the overall abundance of the germinable seed bank that are

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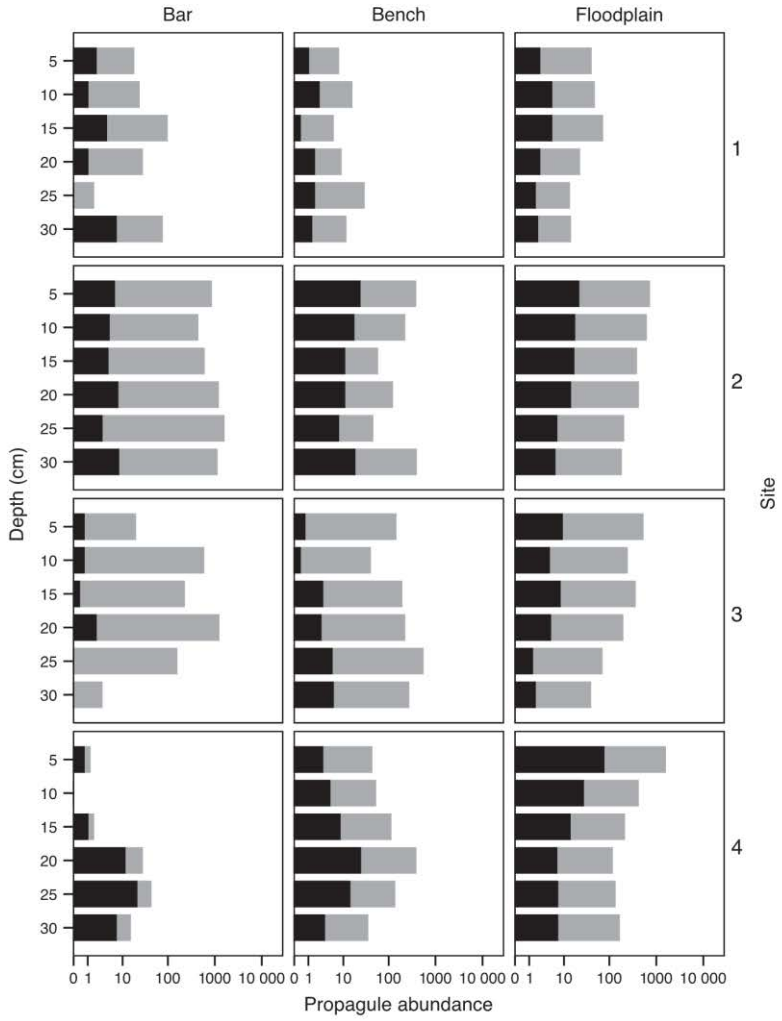

Fig. 3 Mean native (grey) and exotic (black) propagule abundance per 450-cm^3 sample of the germinable seed bank in relation to depth. Results are shown for each geomorphic unit type: bar, bench and floodplain, in each of four study reaches.

worth noting. The abundance of native and exotic propagules at each depth (0–5 cm, 5–10 cm, 10–15 cm, 15–20 cm, 20–25 cm and 25–30 cm) within bars, benches and floodplains for the four sites is shown in Fig. 3. The two downstream reaches (sites 2 and 4) had a greater proportion of exotic propagules and species than the two upstream sites. Overall, Sites 1 and 4 had significantly fewer seedlings emerge from all the samples than did Sites 2 and 3. Therefore, in all statistical analyses, the random factor site had a significant effect (e.g. GLMM: $F_{3,122}$= 18.896, P = <0.001).

Patterns of cumulative species richness with depth (Fig. 6) showed that, for each unit sampled, new species were encountered with each successive depth sample. Interestingly, richness counts could vary greatly between units, as seen for the Site 4 data where richness was least in bars and greatest in floodplain samples. Conversely, at Site 1, richness counts were very similar between all three geomorphic unit types. For all geomorphic units, new species consistently emerged from samples at increasing depth to 30 cm, with little evidence of plateauing. This suggests that the composition of the germinable seed bank is quite variable with depth.

Discussion

We examined the vertical distribution of the soil and sediment seed bank for a range of geomorphic units in the riparian zone of a sand-bed system. In support of

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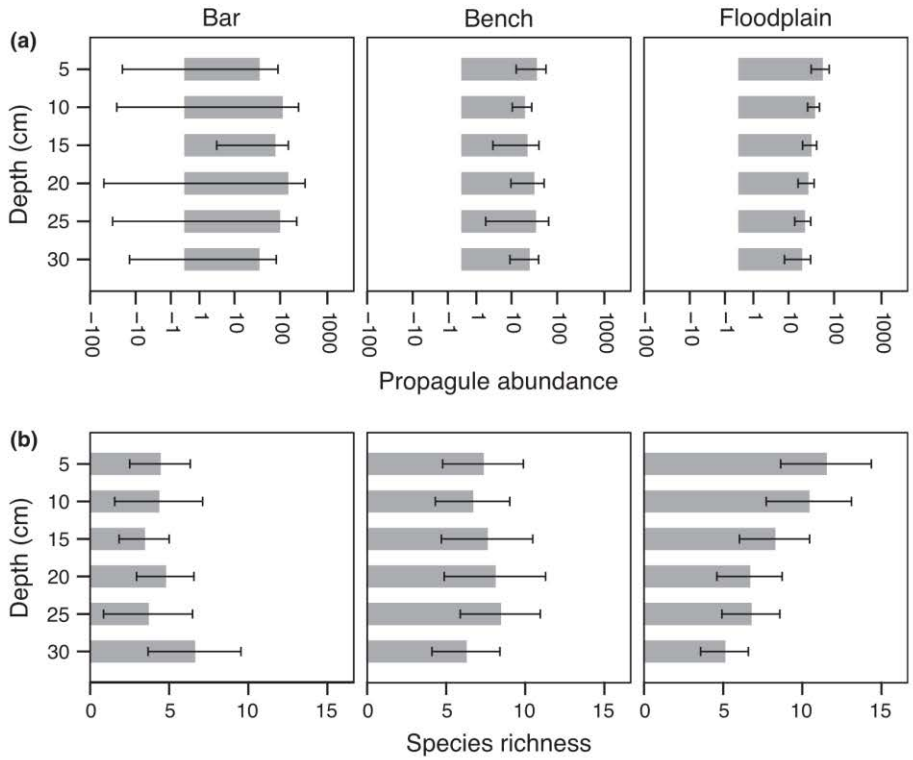

Fig. 4 A comparison of (a) mean propagule abundance and (b) mean propagule species richness per 450-cm^3 sample of the germinable seed bank at 5-cm intervals to a depth of 30 cm in bars, benches and the floodplain. Error bars represent two standard errors.

our hypothesis, propagule abundance and species richness were highly variable with depth in both bars and benches. In contrast, the germinable seed bank declined with depth on the floodplain. We predicted that the seed bank of bars would be less abundant and species rich than those of benches, due to continual reworking by low water flows. We found that bar seed banks were significantly less species rich, although propagule abundance was highly variable, and greater on average than that within benches and the floodplain.

Few studies have examined the depth distribution of seed banks in riparian systems. Many authors assume shallow seed banks, and rapid declines in seed numbers with depth have been found in a range of environments, including lakeshores (e.g. > 80% of seeds in top 5 cm of sediment; Nicholson & Keddy, 1983) and wetlands (reviewed in Leck, 1989). Similarly, both Grillas *et al.* (1993) and Bonis & Lepart (1994) reported exponential reductions in seed abundance with depth in temporary marshes. In the latter study, however, some seeds were found at a depth of 12 cm. In contrast, Berge & Hestmark (1997) and Abernethy & Willby (1999) found no significant difference in seed numbers between the top and bottom 5 cm of a 10-cm sediment sample from wetlands and an abandoned stream channel, respectively. Furthermore, in some environments, seed banks have been shown to extend into much deeper sediments. High seed numbers were found to depths of 35 cm in glacial prairie marsh sediments (Van Der Valk & Davis, 1979), and Leck & Simpson (1987) found many seeds at 32 cm in a tidal freshwater marsh.

There has been surprisingly little seed bank research conducted within river channels. As discussed previously, several factors influence the vertical development of seed banks within these systems. Inundation of a surface may result in the deposition, reworking or erosion of sediment, depending on factors such as stream power and the cohesion of the sediment. Sediment deposition results in the delivery of seeds via hydrochory to the seed bank, although reworking may disturb seeds within sediment, and erosion may completely remove seeds. Additional seeds are provided by the surrounding environment, although seeds may also be lost due to seed germination, predation and mortality. It is the pro-

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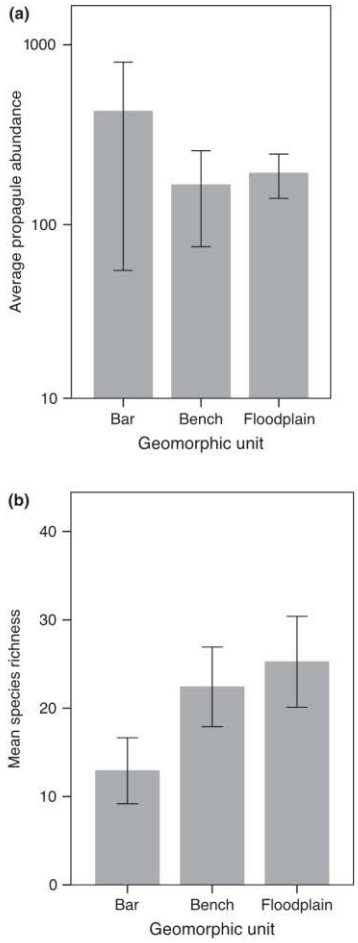

Fig. 5 Mean (a) abundance and (b) species richness of the germinable seed bank to a total depth of 30 cm compared between bars, benches and the floodplain combined across the stream reaches of the four study sites. Error bars represent two standard errors.

portional influence of each of these factors that will determine both the form of the geomorphic unit and the vertical distribution of the seed bank within it. Discussion of these factors is largely absent, with the exception of Grillas *et al.* (1993) who assessed disturbance of the seed bank in the form of flooding and drawdown of flood waters, and/or the movement of animals. Similarly, Bonis & Lepart (1994) report on low sedimentation rates influencing the depth of the seed bank.

Our results support the hypothesis that the abundance and species richness of seeds in both bars and benches are highly variable with depth (Figs 3 & 4a). Bars and benches are essentially depositional features, and both are likely to store variable quantities of seeds, depending on the hydrochoric seed input at the time of each deposition event. Benches are formed and reworked over decadal timescales (Erskine & Livingstone, 1999; Erskine *et al.*, 2009) and tend to form during small-to-moderate floods when bedload sediment is deposited as floodwaters rise, and finer suspended sediment deposited as waters recede (Brierley & Fryirs, 2005). It is during both these stages that hydrochoric propagules will be incorporated into the bench seed bank. It takes a larger flood to cause reworking of the bench surface, and a catastrophic flood to cause significant erosion and thus destruction of benches (Erskine, 1996). Exposure time between inundating flows allows the growth of vegetation, which increases sediment cohesion and thus resistance to erosive forces (Johansson & Nilsson, 1993; Corenblit *et al.*, 2008; O'hare *et al.*, 2012). Considering the timescales of bench formation and destruction, as well as their capacity to capture sediment, benches have the potential to build deep, substantial seed banks. For example, we found no evidence of declining seed numbers with depth (Fig. 4a), which could have indicated the presence of older sediments within which seed mortality may have reduced propagule numbers (e.g. Van Der Valk & Davis, 1979).

We hypothesised that seed abundance and species richness would be lowest in bars due to their position and potential for frequent reworking, even by low flows. This was indeed the case for the latter, but there was significant bar-to-bar variation. We suggest that this variation may be due to several factors. Firstly, while frequent inundation has been found to increase seed abundance, flows over bars may have a flushing effect on seeds, effectively reducing the abundance and species richness of the seed bank (Capon & Brock, 2006; Gurnell *et al.*, 2007a). For example, Gurnell *et al.* (2007a) found frequent turnover of seeds within the seed bank of gravel and sand-bed rivers, which supports the capacity of flowing water to move or flush seeds and sediments. We found that the 0- to 5-cm layer of sediment in bars often contained lower propagule numbers than deeper layers (Fig. 3), which may be evidence of seed flushing via surface sediment reworking. Secondly, Gurnell *et al.* (2007a) also found that the highest seed numbers on the channel bed were found in sediments accumulated around vegetation. As sand bars are accumulations of sediment formed by changes in hydrology in response to river bed morphology and planform, or the presence of obstacles (Brierley & Fryirs, 2005), it is evident that these units may also incorporate high seed numbers. We found that, on average, the species richness of the seed bank was greatest in the deepest bar sediments. Some

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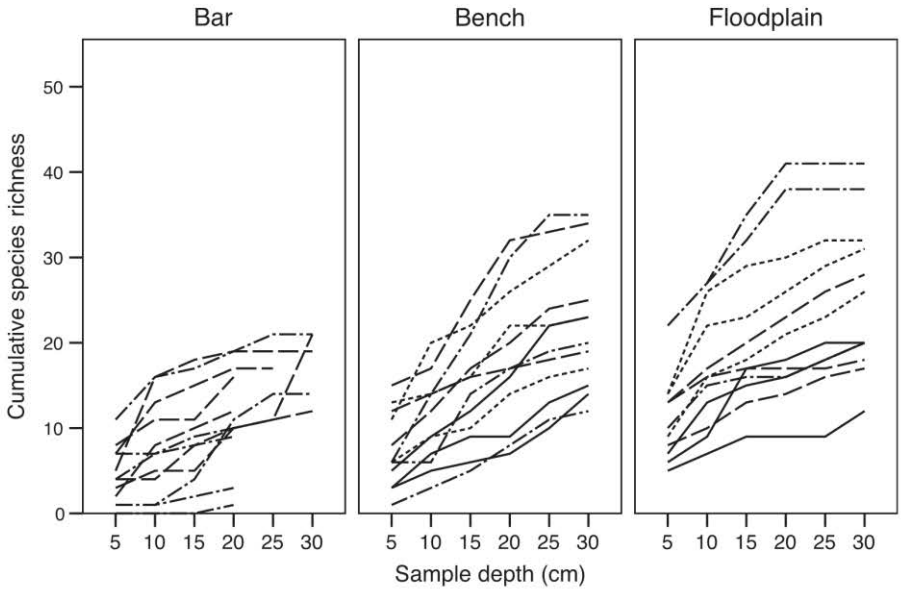

Fig. 6 Cumulative species richness, that is, the total number of species encountered in the seed bank from the sediment/soil surface to each successive depth sample (i.e. 0–5, 0–10, 0–15, 0–20 0–25 and 0–30 cm) in bars, benches and floodplain. Line types correspond to site, with three replicates of each geomorphic unit at each site presented.

bars, however, contained few if any seeds and others contained large depositions of species such as *Gratiola peruviana* and *Isolepis inundata*. As both these species are semi-aquatic, and known for abundant seed production (Stevens, 1932; Holmes & Cowling, 1997), it is possible these large depositions were sourced from plants growing on the bars, as local vegetation often provides a large component of the seed bank (Gurnell *et al.*, 2006b; James *et al.*, 2007).

Our results support the hypothesis that the seed banks of the floodplain resemble those of terrestrial environments, where propagule abundance often declines with depth (Fig. 3). We suggest that this pattern is the result of low rates of sediment deposition (and thus infrequent deposition of hydrochoric seeds) and infrequent disturbance preventing seed redistribution and germination. Each of the study reaches had well-developed floodplain vegetation with medium-to-large trees present. All reaches had a moderate to dense ground cover of grasses and herbs, suggesting a substantial time since a flood event large enough to cause significant scouring or sediment deposition on these surfaces. Interestingly, although propagule abundance declined with depth, we still found large numbers of seeds in sediments as deep as 30 cm, in contrast to the rapid declines in abundance commonly reported in terrestrial environments (Dalling, Swaine & Garwood, 1997; Swanton *et al.*, 2000; Traba *et al.*, 2004). Deeply deposited seeds were dominated by Juncaeae and Cyperaceae wetland species, which can form prolific and persistent seed banks and may indicate deposition during one or more flood events (Bakker *et al.*, 1996; Allessio Leck & Schütz, 2005; Boudell & Stromberg, 2008b; Stromberg, Boudell & Hazelton, 2008).

In the absence of significant disturbance of the floodplain, we can be confident that deeper sediments are older. As such, we would also expect that the number of viable propagules should decrease with depth, as they succumb to mortality and decomposition over time (Goodson *et al.*, 2002), and that deeper sediments should have a greater proportion of seeds of species that display some degree of dormancy or seed persistence. Many such species are found within riparian environments due to the selective pressure of fluctuating environmental conditions (Cohen, 1966; Venable & Brown, 1988). We found that the species richness of the seed bank generally decreased with depth and that the deepest sediment samples had the lowest species richness (Fig. 4). Of 12 species that we found primarily at depths of 30 cm, eight were sedges (Cyperaceae) or rushes (Juncaceae) and came from families where seed persistence, dormancy or specific germination requirements are prevalent (Schütz, 2000; Leck & Schütz, 2005). In contrast, bench sediments

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are generally much younger than floodplain sediments (Webb, Erskine & Dragovich, 2002), and bars are reworked at higher frequencies, which may explain why the patterns of species richness did not decline with depth in bars or benches (Fig. 4b). Interestingly, *cumulative* species richness was highly variable with depth in all geomorphic units (Fig. 6), suggesting that the *composition* of the seed bank was highly variable within all units.

Implications for riparian vegetation management and restoration

The consideration of soil seed banks in the management of riparian vegetation is a fairly recent phenomenon (Goodson *et al.*, 2001; Washitani, 2001; Richardson *et al.*, 2007), although compositional information on the seed bank can provide an indication of the resilience and recovery potential of the system (Williams *et al.*, 2008). Our results suggest that there is high potential for the seed bank to provide rapid regeneration of vegetation on bars, benches and floodplains following flows of a magnitude sufficient to disturb or erode sediment to at least 30 cm. Furthermore, the mix of species may change depending on the depth to which sediment has been eroded. The high number of perennial species, including known bank-stabilisers such as *Lomandra longifolia*, may rapidly increase the stability of geomophic surfaces after disturbance, providing suitable conditions for the establishment of other species and vegetation succession (Hopfensperger, 2007). Similarly, both the annual and perennial plants derived from the seed bank have the potential to increase roughness and enhance sediment storage (particularly in benches) within channels that have been highly disturbed or altered, and are showing signs of geomorphological recovery (Erskine *et al.*, 2009; Fryirs *et al.*, 2009, 2012). Subsequent seed inputs from hydrochory and seed rain will contribute to these processes, as the time since disturbance increases.

Seed banks are increasingly recognised as a potential source of seed in the revegetation and restoration of degraded ecosystems (Middleton, 2003; Richter & Stromberg, 2005; Jensen *et al.*, 2008). For example, one such application involves the transplantation of soil or sediment collected from a reference ecosystem to a degraded site after some change in the disturbance regime (e.g. fencing to restrict livestock entry, or removal of a dominant invasive plant) to allow natural regeneration from the seed bank (e.g. Nishihiro, Nishihiro & Washitani, 2006). Our research can inform sensible approaches to sediment sampling in river systems for these purposes. For example, a greater diversity of seed species may be captured by sampling sediment to depths beyond 10 cm. Furthermore, benches and the floodplain contain much more consistent seed numbers with higher species richness than bars, making the former preferable units for harvesting seed banks.

A final important factor for consideration is the longevity of seed banks within riparian systems. The timescales at which riparian seed banks are formed in different geomorphic units and the influence that environmental conditions will have on seed longevity will affect both species richness and the abundance of seed bank propagules (Wilson, Moore & Keddy, 1993; Thompson, 2000). Ultimately, in the absence of disturbance, the number of viable seeds within buried sediments will decrease over time (Conn, Beattie & Blanchard, 2006). This has implications for the capacity for these deeper riparian seed banks to contribute to vegetation after significant periods of time without reworking, for example after a prolonged period of drought, or low flows caused by flow regulation. As such, the frequency by which propagules are incorporated into, and released from, the seed banks of these different geomorphological structures has interesting implications for temporal variability in seed inputs within riparian systems, and the development of diverse riparian plant communities.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 List of species identified from the seedling emergence study, with details on their family, origin, longevity and growth form.

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Chapter 3

Riparian seed banks and sedimentology

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Can the sedimentological and morphological structure of rivers be used to predict characteristics of riparian seed banks?

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ABSTRACT

Seeds are transported by flowing water along with sediment and organic matter and form seed banks within the fluvial landforms (or geomorphic units) of river systems. Fluvial processes commonly result in observable gradients in sediment characteristics with elevation above the channel bed. This study aims to investigate spatial variability in seed bank characteristics that may be attributed to fluvial processes. We compared the extent to which four riparian seed bank characteristics (abundance, species richness, seed mass, and seed shape) are correlated with (1) fluvially influenced gradients in sediment character (percentage of organic matter [organic %], median particle size [D_{50}], percentage of fine particles [% fines], and the combined percentage of sand and gravel [% sand/gravel]); and (2) three geomorphic unit types that form with increasing elevation above the channel bed: bars, benches, and the floodplain. Seed bank abundance and species richness were weakly yet significantly correlated with sediment gradients, significantly increasing with increasing % fines and decreasing % sand/gravel. Seed bank species richness also significantly increased with increasing organic % and decreasing D_{50}. Conversely, seed abundance was highly variable, and relationships between sediment qualities and seed mass and shape were nonexistent. We suggest that hydrological factors such as inundation frequency, operating most clearly at the geomorphic unit scale, ultimately drive spatial variability in riparian seed bank characteristics by (1) *directly* influencing seed inputs and losses from seed banks via erosion and deposition, which is complicated by species-specific differences in seed morphology; and (2) *indirectly* influencing seed inputs and losses by mediating seed germination and mortality and the establishment success of plants, through impacts on sediment moisture and organic matter content. Further complexity is added by nonfluvial seed inputs from established vegetation. The net result of these influences tends toward decreasing potential for seed losses and increasing potential for seed inputs associated with the reduction in inundation frequency observed from bars to the floodplain. For those assessing the potential of the seed bank as a seed source for revegetation, sediment sampling for seed bank assays targeted at organic flood debris, or fine, organic-rich sediments such as those typically associated with benches and the floodplain, should elicit useful estimations of seed bank composition.

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1. Introduction

Naturally occurring seed banks (also known as *propagule banks* when spores and other vegetative fragments are included) form in soil and sediment as plant species collectively display a diverse array of seed dormancy mechanisms and/or require particular environmental cues (e.g. prolonged submersion, high or low temperatures), before seed germination will occur (Fenner, 1992). The seed bank plays a strong ecological role in the regeneration of vegetation. This is particularly true in environments subjected to recurrent disturbance, as germination from the seed bank can be temporally staggered, allowing multiple chances for a species to establish (Bonis et al., 1995; Jutila, 2001; Brock et al., 2003; Bornette et al., 2008). As such, there is a drive to understand seed bank properties for the field of ecosystem restoration (e.g., Goodson et al., 2001; Middleton, 2003; Richter and Stromberg, 2005; Robertson and James, 2007; Jensen et al., 2008; Vosse et al., 2008).

In river systems, interactions between established vegetation, unidirectional water flow and the movement of sediment can produce seed bank features that are particularly characteristic. For example, seed bank abundance or composition has been shown to vary with lateral distance from the river channel, with elevation above the channel bed (e.g. Goodson et al., 2002; Capon and Brock, 2006; Webb et al., 2006; Gurnell et al., 2008; Corenblit et al., 2009) and with the depth of burial in sediment (O'Donnell et al., 2014). Riparian seed banks also often display higher species richness in comparison to established vegetation, attributed to consistent seed inputs from upstream vegetation

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assemblages in addition to that contributed by the vegetation that is locally present (Jansson et al., 2005; Vogt et al., 2006; O'Donnell et al., in press).

Hydrochory, the transport and deposition of seeds by water, is likely to be most influential in the development of riparian seed banks (Jansson et al., 2005; Gurnell et al., 2006). Floating seeds are often transported with a range of other organic debris on the water surface (Skoglund, 1990; Hupp, 1992; Pettit and Froend, 2001). Submerged seeds may behave as a component of mineral sediment, either saltating along the channel bed or moving with suspended sediment, depending on stream power (Gurnell et al., 2007; Moggridge et al., 2009). Seeds deposited on riparian surfaces by other dispersal mechanisms such as wind, animals, and gravity may also be remobilised by flowing water.

Fluvial processes are well known to impart observable gradients in sediment qualities. For example, reductions in sediment grain size (e.g. from sand to silt) and increases in organic matter content are generally observed distally over the floodplain (Powell, 1998; Brierley and Fryirs, 2005) or across different geomorphic unit types with increasing elevation from the channel bed (e.g., bars, benches, and the floodplain; Osterkamp and Hupp, 1984; Brierley and Fryirs, 2005). These sediment gradients are related to stream competence and the hydraulic sorting of sediment particles of different mass and shape that occur during entrainment, transport, and deposition. The organic content of sediment may also indicate the frequency of inundation leading to sediment reworking and deposition, or conversely, the exposure time between inundation events during which organic matter may accumulate (Wilson and Keddy, 1986; Steiger and Gurnell, 2002; Bornette et al., 2008). Given that buoyant seeds often affix to floating organic matter and that submerged seeds essentially make up a component of suspended or bedload sediment (Hupp, 1992; Gurnell et al., 2007; Moggridge et al., 2009), seed banks that develop in riparian sediments may similarly reflect these fluvially generated processes and patterns. Is this fluvial signal likely to be preserved in the seed bank despite seed inputs and losses attributable to other processes?

Previous studies attempting to observe a fluvial signal in seed bank qualities have had mixed results. Wilson et al. (1993) observed seed bank abundance to increase with sediment organic matter content in a Canadian freshwater marsh. In deposited sediments along English rivers, Goodson et al. (2003) and Gurnell et al. (2008) also observed a positive relationship of seed abundance with sediment organic content and a negative relationship with elevation. The latter study found species richness also to be correlated with sediment organic content. Negative relationships between seed abundance and sediment grain size were observed by Gurnell et al. (2008) and also by Oishi et al. (2010) in a gravel-bed river in Japan. In contrast, two seed bank studies conducted in Australian lake and river systems failed to find patterns in species richness or abundance related to the elevation gradients along which changes in sediment are commonly observed (Webb et al., 2006; Williams et al., 2008). Flume and seed settling experiments investigating the hydraulic sorting and differential deposition of seeds have shown submerged seeds across a wide spectrum of masses (0.002–38 mg) to have similar settling velocities to fine sandy sediments or for seeds to settle at velocities similar to sediments of comparable mass (Nakayama et al., 2007; Chambert and James, 2009; Yoshikawa et al., 2013). Buoyant seeds, and especially those with appendages however, are greatly affected by factors such as wind drift and boundary conditions (e.g. the qualities of vegetation present) (Chambert and James, 2009; Yoshikawa et al., 2013).

Our objective was to detect spatial variability in seed bank characteristics and seed traits that may be attributed to fluvial processes across four sand-bed stream reaches in the lower Hunter Valley, in southeastern Australia. Theoretically, fluvial processes should result in (i) increases in seed bank abundance and species richness with sediment organic content, as seeds contribute to organic debris carried and deposited by flowing water; (ii) decreasing seed bank abundance with increasing sediment particle size, reflecting a higher potential for seeds to be flushed from between larger particles (Oishi et al., 2010; O'Donnell et al., 2014); (iii) more large and heavy seeds in coarser sediments at lower elevations in the channel and lighter seeds in finer sediments at higher elevations if seeds are sorted by mass akin to sediment particles (e.g. Chambert and James, 2009; Nilsson et al., 2010); and (iv) more elongate seeds in finer sediments as a result of increased buoyancy and thus floating ability and fewer round seeds in larger grained sediments, from which they may be more easily flushed (Cerdà and Garcia-Fayos, 2002; García-Fayos et al., 2010). Specifically, we asked whether seed bank characteristics (abundance and species richness) and seed traits (seed mass and seed elongation) are correlated with the fluvially influenced sediment gradients associated with organic matter content and particle size that are observable from bars to benches to the floodplain. Previous studies in this riparian system found seed bank abundance to be highly variable across geomorphic units, whilst species richness was always lower in bars but comparable between the benches and floodplain (O'Donnell et al., 2014, in press). Based on the findings of this research, we aim to determine whether geomorphic units, or sediment gradients, represent a more practical scale for predicting seed bank qualities.

2. Regional setting

2.1. Study reaches

This study was conducted in the Wollombi Brook subcatchment situated in the lower Hunter Valley, New South Wales, Australia (Fig. 1). The Wollombi Brook drains a sub-catchment of ~470 km^2 and receives ~900 mm mean annual rainfall. Wollombi Brook is characterised by high flood variability and flashy floods facilitated by steep topography and cleared floodplains (Erskine, 1996; BMT WBM, 2010). Rivers within the subcatchment are sand-dominated, derived from the Triassic intercalated sandstone and shale that comprise the catchment. We selected four stream reaches to study: an upper reach and middle reach of Watagan Creek, the 94-km major tributary of Wollombi Brook (reaches 1 and 2, respectively) and an upper reach and middle reach of Wollombi Brook itself (reaches 3 and 4, respectively) (Fig. 1). These reaches are partly confined, planform-controlled with channel bed slope ranging from 0.0039 m/m in upstream reaches to 0.0009 m/m in downstream reaches.

2.2. Flood history and geomorphology

Historical adjustments to Wollombi Brook and its tributaries are well documented elsewhere (e.g. Erskine, 2008; Erskine and Melville, 2008; Fryirs et al., 2012). Parts of the system have been subject to historical channel incision and widening induced by widespread clearance of floodplain vegetation that occurred post-European settlement and a series of floods that occurred in the 1940s and were the largest on record (Erskine, 1996, 2008). Since this time, many of the severely widened channels have undergone extensive channel contraction through the formation of depositional benches (Erskine et al., 2009; Fryirs et al., 2012). Since the 1980s, an increase in vegetation coverage within the channel and on the floodplain has greatly increased the stability of streams within the catchment (Erskine et al., 2009). The second largest flood on record in 2007 resulted in significant reworking of sediment within the channel but little overall geomorphic change in the riparian zone (Fryirs et al., 2012).

We chose to investigate the sedimentology and seed bank characteristics of three distinct and commonly occurring geomorphic units: bars, benches, and floodplains. Bars were bank-attached units comprising noncohesive medium and coarse sands, situated slightly higher than the low flow water level. Bars were generally sparsely vegetated with little accumulation of organic matter. Benches were bank-attached depositional features that were elevationally variable across the four

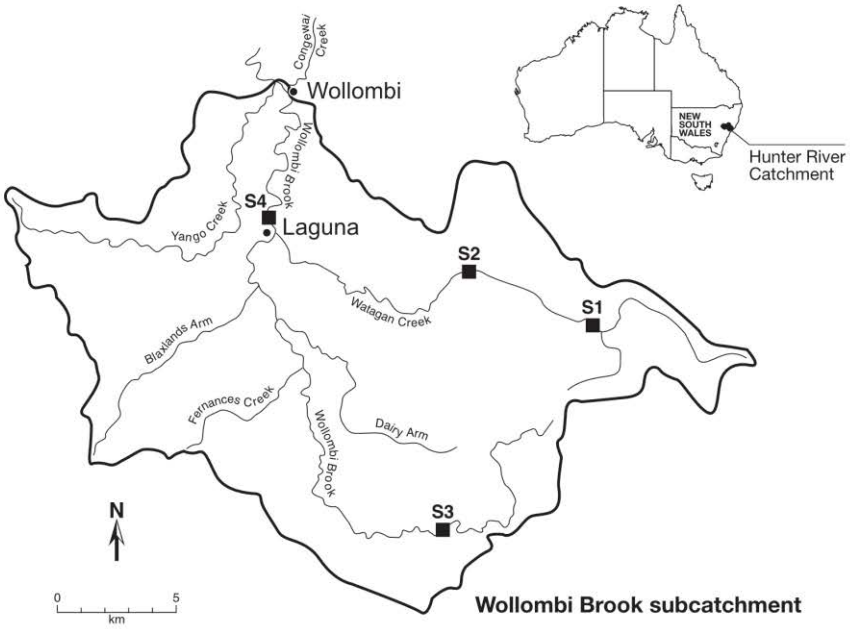

Fig. 1. Location of study reaches. Map of the Wollombi Brook subcatchment situated in the lower Hunter River catchment of New South Wales, Australia. S1–S4 indicate the location of the four study reaches, situated along Wollombi Brook and Watagan Creek.
Map modified from Erskine and Melville (2008) and reproduced from O'Donnell et al. (in press).

study reaches but always higher than bars. These units were composed of medium to fine sands and displayed established vegetation ranging from new recruitment on more recent sand deposits to diverse stands including shrubs and trees. The floodplain adjacent to the channel was composed of fine sands and loam and was generally well vegetated, with moderate to dense accumulations of organic material (see also O'Donnell et al., 2014, in press). Based on the hydrological modelling of streams in the upper Wollombi Brook catchment by Fryirs et al. (2012), bars in the catchment are generally inundated by a 1:1 to 1:2 year flood event, benches inundated between a 1:2 to 1:5 year flood event, and the floodplains across the study reaches inundated between a 1:5 and 1:10 year flood event.

3. Materials and methods

3.1. Soil and sediment sampling

At each of the four study reaches, three bars, three benches, and three areas of floodplain were selected, and sediment sampled from each in May 2011. At each sampling location ~1000 cm^3 of sediment was collected from each of three small randomly located trenches dug to a depth of 30 cm and then pooled into a single sample of ~3000 cm^3. Several bars were only sampled to a depth of 20 cm because of water infiltration. From each pooled sample, ~2700 cm^3 was subjected to a glasshouse seedling emergence study, used to determine the composition of the seed bank. The samples were refrigerated at 4 °C until the emergence study commenced in May 2011. The remainder of each sample was set aside for sediment analysis.

3.2. Seed bank analysis using seedling emergence technique

Each 2700 cm^3 sediment sample collected for each geomorphic unit replicate was divided into six equal portions, and each portion was spread at an even thickness (~2 cm) over a base of washed river sand in seedling trays measuring 10 × 13 cm. The trays were randomly allocated on benches within a glasshouse in the Macquarie University plant growth facility. The seedling trays were subjected to natural cycles of daylight and mist watered as required to keep the samples moist at all times. Each seedling that emerged was allowed to develop until identification to species level was possible, documented, then removed. The samples remained in the glasshouse for approximately six months, when no further germination had been observed in any of the samples for two weeks. The total number of individuals of each species was tallied for each geomorphic unit sample by combining the results of the six seedling trays.

3.3. Sediment and seed characteristics

Four sediment characteristics were measured using 85–756 g of each of the 36 pooled sediment samples. The average total percent of organic matter (organic %) for each geomorphic unit sediment sample was determined from three samples subjected to the loss on ignition technique (Rayment and Lyons, 2011). Median sediment particle size (D_{50}) was estimated using cumulative 0.5ø weight fractions up to −3ø (8 mm). The percent of fine sediment particles (% fines) (particle size < 4ø/0.0625 mm), including silt and clay, was determined using wet sieving and weight upon drying. The proportion of sand and gravel (% sand/gravel) (particle size > 4ø/0.0625 mm) was determined by dry sieving. Sand and gravel were combined as gravel was present in only 14 of the 36 samples and was highly variable in quantity, making it unsuitable for analysis in isolation.

Data on average seed mass (mg) and seed elongation (seed length/width) were collected for as many of the species identified in the seed bank as possible (seed mass: $n = 98$; seed elongation: $n = 64$). Most seed mass data were obtained from the Kew Seed Information database. Seed length and width data and additional seed mass data were collected from a large range of published literature and various online sources.

3.4. Data analysis

The relationships between each of the four sediment variables and each of the four seed bank characteristics (seed bank abundance, species richness, average seed mass, and average seed elongation) were investigated using pairwise linear regression (LR) analyses for each pairwise seed bank–sediment comparison. Data for each sediment variable required transformation to achieve a normal distribution prior to analysis (organic %: square root transformation; D_{50}: Log_{10} [datum × 100]; % fines: Log_{10} [datum × 100]; % sand/gravel: Log_{10} (reflected data × 10), i.e., Log_{10} [10 × [[1 + largest value of original variable] − [original value of variable]]]). The data for seed bank abundance was also normalised by Log_{10} transformation. Based on the results of the seedling emergence experiment, we calculated for each seed bank sample the average seed mass (mg/seed) and seed elongation (length/width) of (i) the species detected in the sample (species-level analysis) and (ii) all the seeds detected in the sample (abundance-weighted analysis), using the available species' seed mass, length, and width data that were obtained from the literature. Data on average seed mass and seed elongation for species and total seeds for each sample were Log_{10} transformed. After transformation, the average species seed elongation data still slightly deviated from a normal distribution (Kolmogorov Smirnov test: $p = 0.037$, Shapiro–Wilk test: $p = 0.028$). We considered this deviation acceptable to continue analysis. These transformed variables were used in all further analyses.

Prior to comparing the seed bank characteristics between the three geomorphic units (bars, benches, and floodplain), we conducted a preliminary analysis to determine whether the sediment characteristics (organic %, D_{50}, % fines, and % sand/gravel) differed significantly between the units across the four stream reaches. We employed General Linear Mixed Modelling (GLMM) using Restricted Maximum Likelihood (REML) for estimation to test for differences between geomorphic units. For each sediment variable we tested the effect of the fixed factor Unit (three levels: bar, bench, and floodplain) nested within the random factor Site (four levels: reaches 1–4). We also tested for any significant site-based differences in the comparative sediment characteristics of bars, benches, and floodplain (Unit * Site interaction).

We aimed to determine the extent to which each sediment variable contributed to any significant differences in seed bank characteristics between bars, benches, and the floodplain. Previous work by O'Donnell et al. (2014) found seed bank abundance to be highly variable, particularly in bars. In the same study, seed bank species richness was found to be significantly lower in bars than benches and the floodplain. For seed mass and elongation we employed GLMMs to test for differences between the units. We first tested the effect of the fixed factor Unit nested within the random factor Site, using REML estimation. We investigated the extent to which each sediment variable contributed to differences in seed bank abundance and species richness between the units, using mixed model Analysis of Covariance (ANCOVA). All regression, GLMM and ANCOVA analyses were conducted in SPSS v. 20. We used the SMATR v. 2.0 program (Falster et al., 2006; Warton et al., 2006) to further investigate the nature of sediment–seed bank relationships between the units for significantly contributing sediment variables. Regression lines were fitted to bar, bench, and floodplain data separately using ordinary least squares regression, and a resampling procedure was used to test for common slopes between the units. For common slopes we tested for elevation shifts and shifts along the common axis between bars, benches, and the floodplain and ran post-hoc multiple comparisons based on Wald tests.

4. Results

4.1. Seedling emergence study results

A total of 9454 seeds were detected and identified in the seedling emergence study across the 36 seed bank samples (bars [$n = 12$]: 5133; benches [$n = 12$]: 1998; floodplain [$n = 12$]: 2324). Large depositions of two species, *Gratiola peruviana* (2583 seeds) and *Isolepis inundata* (2045 seeds) accounted for the large number of seeds detected in bars. In total, 129 species and 49 different families were represented in the seed bank. A variety of growth forms including trees, shrubs, ferns, vines, grasses, sedges, and rushes were present.

4.2. Sediment characteristics of bars, benches, and floodplain

Across the four study reaches, all four sediment characteristics significantly differed between the three geomorphic units (bars, benches, and floodplain) (GLMM, organic %: $F_{11,23} = 3.542$, $p = 0.005$; D_{50}: $F_{11,24} = 4.924$, $p = 0.001$; % fines: $F_{11,24} = 10.963$, $p < 0.001$; % sand/gravel: $F_{11,24} = 10.144$, $p < 0.001$) (Fig. 2A–D). In particular, all four sediment characteristics differed significantly between the floodplain and bars. Benches and the floodplain differed significantly for all sediment variables with the exception of organic %. In contrast, bars and benches showed no significant difference in any of the four sediment variables. Overall, the organic % and % fines increased, and D_{50} decreased from bars to benches to floodplain. The % sand/gravel was comparable between bars and benches but lower in the floodplain. General linear modelling revealed no Unit * Site interactions for any of the four sediment variables, suggesting that these patterns were generally consistent across the reaches. However, the overall organic % of the sediment samples significantly differed between reaches (GLMM, $F_{3,30} = 7.244$, $p = 0.001$).

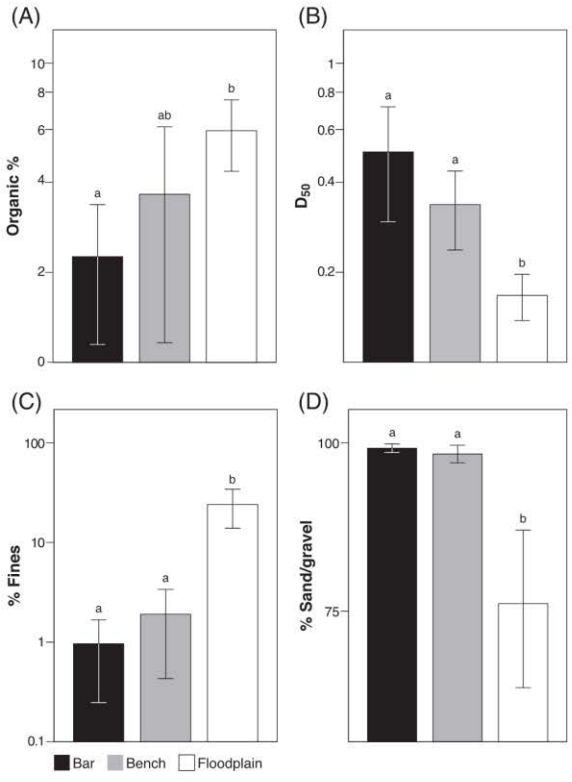

Fig. 2. Comparison of sediment characteristics between geomorphic units. (A) Percentage of organic matter (organic %), (B) median particle size (D_{50}), (C) percentage of fine particles (% fines) and (D) combined percentage of sand and gravel (% sand/gravel) (untransformed data) particles in sediment samples between the geomorphic units bars, benches, and floodplain. Different letters indicate statistically significant differences.

4.3. Relationship between sediment and seed bank characteristics

Investigation of the relationship of the seed bank characteristics with the four sediment variables, pooling across the three geomorphic unit types, yielded mixed results. Seed bank abundance was not significantly related to organic % or D_{50} of the sediment (Fig. 3A,B). However, abundance did increase with increasing % fines ($r^2 = 0.182$, $p = 0.01$) and decreased with increasing % sand/gravel ($r^2 = 0.138$, $p = 0.002$) (Fig. 3C,D). Species richness of the seed bank was significantly related to all four sediment variables, increasing with increasing organic % ($r^2 = 0.2$, $p = 0.006$) and % fines ($r^2 = 0.352$, $p < 0.001$), and decreasing with increasing D_{50} ($r^2 = 0.212$, $p = 0.005$) and % sand/gravel ($r^2 = 0.351$, $p < 0.001$) (Fig. 4A–D). We found no evidence of relationships between the seed traits of the seed bank species and sediment characteristics. Neither the average seed mass nor average seed elongation, calculated on a per-species basis and on an abundance-basis, varied significantly with any of the four sediment variables.

Three of the sediment characteristics (D_{50}, % fines, and % sand/gravel) were significantly correlated with differences in seed bank abundance between bars, benches, and the floodplain (Fig. 3B–D), with D_{50} contributing most strongly (ANCOVA: D_{50}: $F_{11,11} = 6.319$, $p = 0.002$; % fines: $F_{11,11} = 3.248$, $p = 0.031$; % sand/gravel: $F_{11,11} = 3.258$, $p = 0.031$). Median particle size, % fines, and % sand/gravel each had consistent relationships with seed bank abundance across the geomorphic units (SMATR, common regression line and slope). However, bar, bench, and floodplain samples were separated along the regression line, reflecting their sedimentological differences (Wald χ^2, $df = 2$; $D_{50} = 39.742$, $p < 0.001$; % fines = 103.25, $p < 0.001$; % sand/gravel = 99.257, $p < 0.001$). Pair-wise Wald tests confirmed that benches had marginally lower D_{50} and marginally higher % sand/gravel than bars. Similarly, floodplains had lower D_{50} and % sand/gravel and higher % fines than bars and benches (Fig. 3B–D).

Two sediment characteristics: organic % and D_{50} were significantly correlated with lower seed bank species richness in bars compared to benches and the floodplain (ANCOVA, organic %: $F_{11,11} = 4.336$, $p = 0.011$; D_{50}: $F_{11,11} = 3.297$, $p = 0.03$). Both had consistent relationships with seed bank species richness across the three unit types (Fig. 4A,B). The sedimentological differences between bar, bench, and floodplain

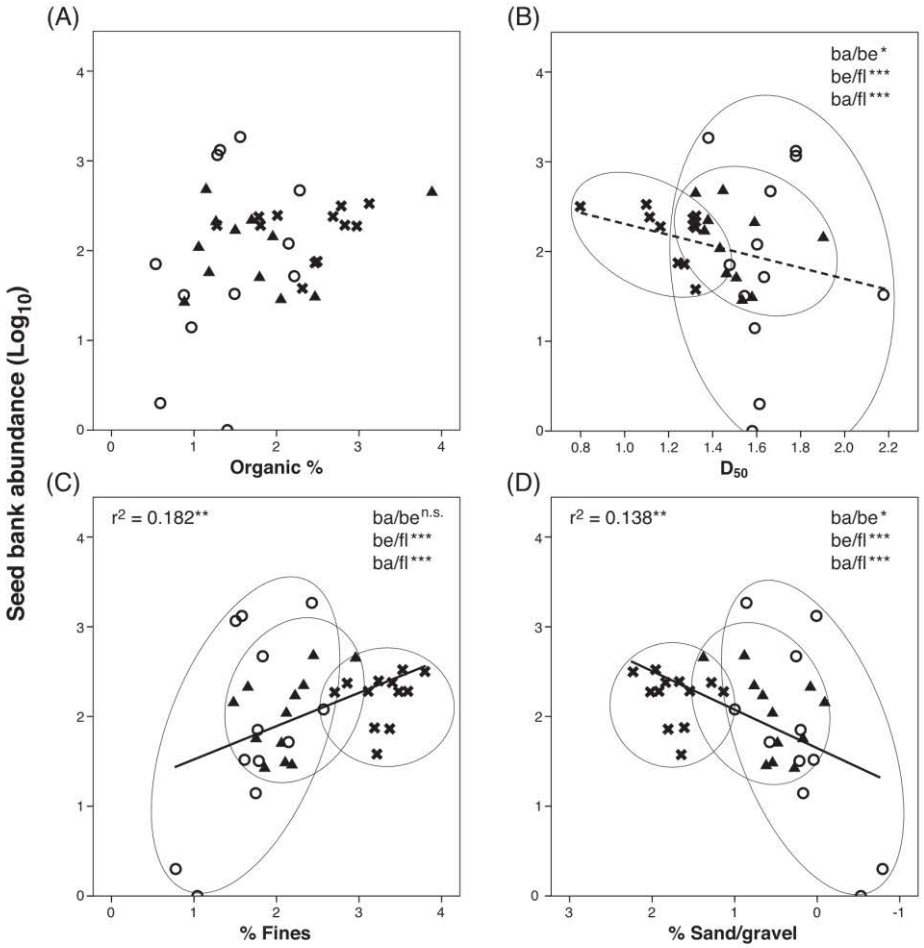

Fig. 3. Relationships between seed bank abundance and four sediment variables. (A) Percentage of organic matter (organic %), (B) median particle size (D_{50}), (C) percentage of fine particles (% fines), and (D) combined percentage of sand and gravel (% sand/gravel) particles in sediment samples. Solid lines and r^2 values indicate significant correlations. For sediment characteristics significantly contributing to significant seed bank abundance differences between geomorphic units: bars, benches, and floodplain (D_{50}, % fines, and % sand/gravel), samples are grouped based on geomorphic unit type (O bar; ▲ bench; × floodplain). Pairwise comparisons between bar (ba), bench (be), and floodplain (fl) indicate the significance of sedimentological differences between units (shifts along the common regression slope). Dashed line in (B) indicates common (but not significant) regression slope for D_{50}. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, n.s. — not significant.

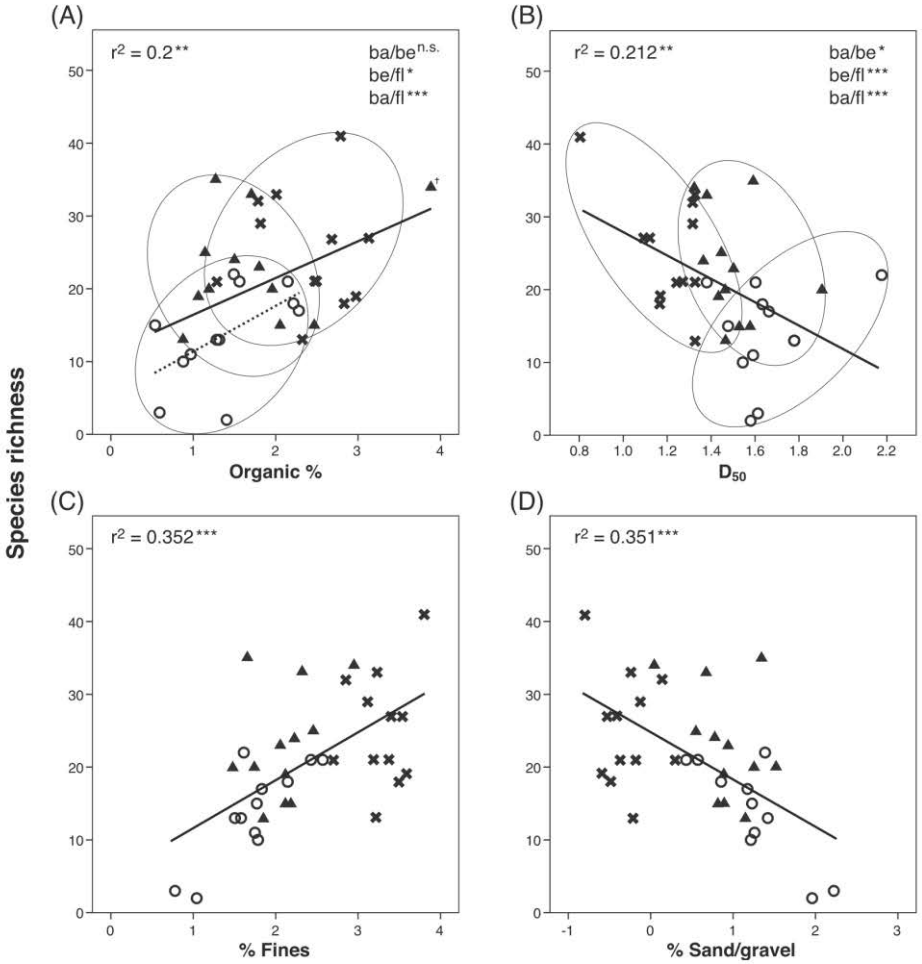

Fig. 4. Relationships between seed bank species richness and four sediment variables. (A) Percentage of organic matter (organic %), (B) median particle size (D_{50}), (C) percentage of fine particles (% fines), and (D) combined percentage of sand and gravel (% sand/gravel) particles in sediment samples. Solid lines and r^2 values indicate significant correlations. For sediment characteristics significantly contributing to significant seed bank species richness differences between geomorphic units: bars, benches, and floodplain (fp) (organic % and D_{50}), samples are grouped based on geomorphic unit type (O bar; ▲ bench; × floodplain; † group outlier). Pairwise comparisons between bar (ba), bench (be), and floodplain (fl) indicate the significance of sedimentological differences between units (shifts along the common regression slope). Broken line in (A) indicates relationship between species richness and sediment organic % in bars, which was significantly less elevated than the common slope. $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, n.s. — not significant.

samples were evident in their separation along both regression slopes (Wald χ^2, $df = 2$; organic % = 16.423, $p < 0.001$; $D_{50} = 39.742$, $p < 0.001$) (Fig. 4A,B), but did not account for the observed lower seed bank species richness in bars. Bars were found to have lower seed bank species richness than that expected based on low organic % alone, reflected by a regression slope for the relationship significantly less elevated than that for benches and floodplain (Wald χ^2, $df = 2$, 10.022, $p = 0.007$) (Fig. 4A).

We found no significant difference in the seed traits of the seed bank between the geomorphic units. Neither seed mass nor seed elongation—calculated on either a per-species basis or on an abundance basis—differed between bars, benches, and floodplain (Fig. 5A,B).

5. Discussion

The findings from this study suggest that simple, observable sedimentological qualities related to organic matter content and particle size may be quite useful for distinguishing between areas of high and low seed bank species richness within a river reach. We found that spatially, seed bank species richness was high where finer sediments and high organic matter content occur. These conditions, as expected, were found on floodplains and benches that are elevated above the channel bed. However, relationships between sediment qualities and seed bank abundance were weak, and no relationship was found with seed mass and seed shape. We attribute these findings to the range of complex interactions that influence seed inputs and losses from riparian seed banks, as depicted in Fig. 6. We suggest that geomorphology and hydrology drive spatial variability in riparian seed bank characteristics by (i) *directly* influencing seed inputs and losses from seed banks via erosion and deposition, which is complicated by species-specific differences in seed morphology, and (ii) *indirectly* influencing seed inputs and losses by mediating seed germination and mortality and the establishment success of plants through impacts on sediment moisture and organic matter content. External seed inputs contributed by plants via nonfluvial dispersal mechanisms add further complexity to spatial patterns of riparian seed bank characteristics.

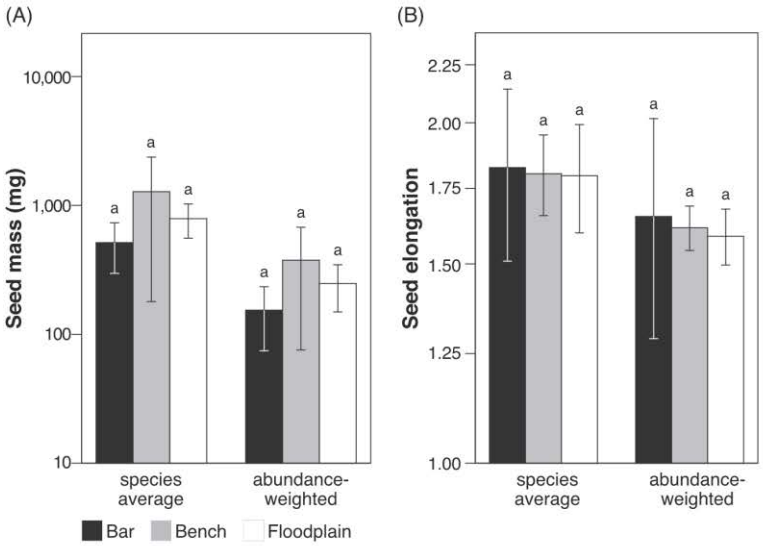

Fig. 5. Average seed bank seed mass and elongation compared between geomorphic units. (A) Mean seed mass for all species (left) and seeds (abundance-weighted, right) detected in the seed bank and (B) mean seed elongation (length/width) for all species (left) and all seeds (abundance-weighted, right) detected in the seed bank for geomorphic units bars, benches, and floodplain. Error bars represent 95% confidence intervals. Different letters indicate statistically significant differences.

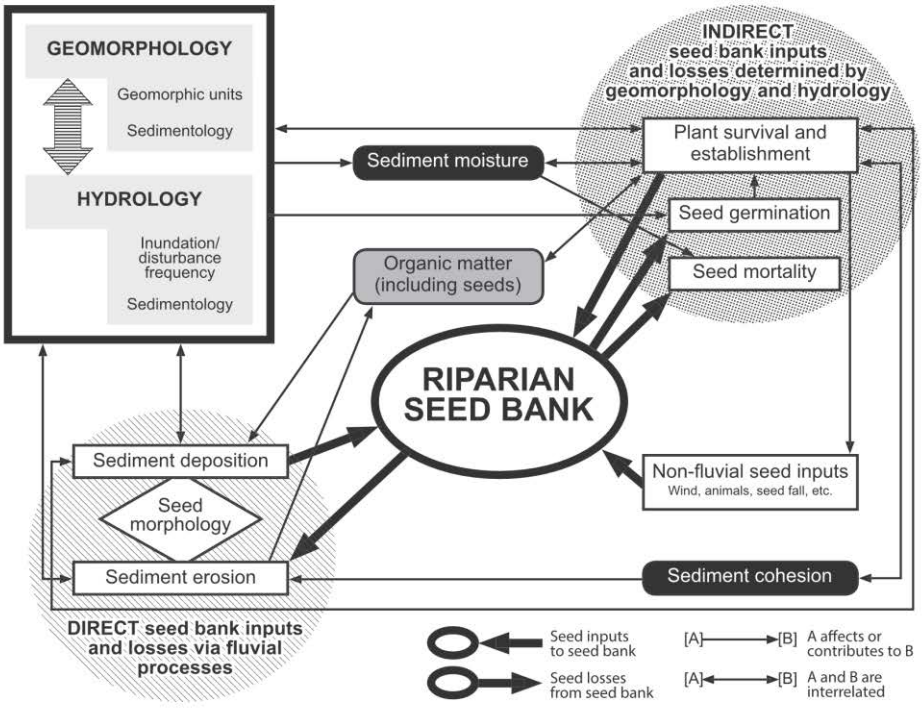

Fig. 6. Factors contributing to spatial variability in riparian seed banks. *Direct seed bank inputs and losses influenced by fluvial processes*: sediment deposition is the main process by which riparian seed banks form. Seeds are deposited along with sediment, as well as organic matter. Erosion results in the removal of seeds from seed bank sediments and contributes seeds to the general pool of organic matter, from which seeds may be redeposited elsewhere. Species-specific differences in seed morphology such as density and shape introduce complexity into seed responses to fluvial erosion and deposition. *Indirect seed bank inputs and losses influenced by geomorphology and hydrology*: variations in hydrological factors such as inundation frequency and duration are most clearly observed at the geomorphic unit scale. Hydrological conditions associated with different geomorphic units, are evident in differences in sediment moisture, which will differentially affect seed mortality and germination, both of which result in seed losses from the seed bank. Inundation resulting in sediment disturbance may encourage germination. Hydrology and fluvial processes affect the survival and establishment of seeds that germinate from the seed bank by determining soil/sediment moisture levels and organic matter content. The development of vegetation assemblages increases the cohesion and stability of sediments, reducing the likelihood or extent of erosion and thus seed removal. Plants surviving to reproductive maturity have the capacity to contribute seeds to the seed bank directly, via fluvial processes, or via animals or wind. *Nonfluvial seed inputs*: These include seeds delivered to seed banks by nonfluvial mechanisms, including wind, animals, and direct seed fall. Parent plants may or may not have established under the influence of fluvial processes.

5.1. Direct influences on riparian seed bank characteristics by fluvial processes

Our aim was to detect relationships between seed bank characteristics and sediment gradients observable across bars, benches, and the floodplain that might reflect direct seed inputs and losses attributable to fluvial processes. We assumed that submerged seeds in the water column are fluvially sorted akin to sediment particles, and floating seeds are deposited along with organic matter. Seed bank abundance and species richness were weakly yet significantly positively related to increasing % fines and decreasing % sand/gravel. Species richness was also weakly positively related to increasing sediment organic % and decreasing D_{50}. Seed bank abundance was highly spatially variable, as found in other studies (e.g. James et al., 2007; O'Donnell et al., 2014; Riis et al., 2014). However, higher seed numbers of greater species richness are typically observed in finer sediments and in sediments containing high organic matter (Wilson et al., 1993; Goodson et al., 2003; James et al., 2007; Gurnell et al., 2008; Riis et al., 2014). Organic flood debris for example is known to contain a diverse array of seeds (Skoglund, 1990; Pettit and Froend, 2001). Furthermore, the low density of organic matter (including seeds) in comparison to mineral sediments causes many seeds to settle out with finer sediments in the waning stages of flow (e.g., Goodson et al., 2003; Gurnell et al., 2008; Riis et al., 2014).

Our observed relationships between sediment and seed bank abundance and species richness adhered to some degree to seed bank patterns predicted by seed responses to fluvial processes. However, we found no direct evidence of fluvial seed sorting according to seed mass or shape. Whilst such sorting is considered possible, species-specific differences in seed size, morphology, density, and buoyancy should greatly increase the complexity of seed responses to hydrological forces and thus affect seed inputs and losses during deposition and erosion events, respectively (Fig. 6). Floating seeds, for example, are subject to wind drift depending on the density, shape, and size of the seed (Nilsson et al., 2002; Boedeltje et al., 2004; Chambert and James, 2009; Soomers et al., 2010; Yoshikawa et al., 2013). Even so, flows of high discharge or stream power are capable of transporting seeds regardless of mass or shape, depositing diverse mixes of propagules in any one location, or eroding large amounts of sediment and releasing all seeds within (Nilsson et al., 2002; Merritt et al., 2010). Seed deposition is further influenced by the nature of the vegetation present on a surface (Fig. 6) (Steiger and Gurnell, 2002; Chambert and James, 2009; O'Hare et al., 2012). The complexity of seed responses to dynamic hydrological and fluvial processes is but one factor influencing spatial variability in riparian seed bank characteristics.

The relative capacities for seeds to be directly deposited or removed from seed banks via fluvial processes should be more clearly distinguished between geomorphic units than along sediment gradients owing to differences in inundation frequency, vegetation establishment, and sediment stability or cohesion between unit types (Fig. 6). Differences in seed bank species richness between bars, benches, and the floodplain were weakly correlated with sedimentological differences between the units (Figs. 4). However, whilst being sedimentologically indistinguishable from benches across the four study reaches, bar seed banks were particularly species poor. Bars are subject to more frequent erosion or sediment reworking, resulting from higher inundation frequencies, limited vegetation cover, and noncohesive sediments, which together increase the likelihood of seeds being flushed from sediments (e.g. Oishi et al., 2010; O'Donnell et al., 2014). Benches and the floodplain (with comparatively moderate and low inundation frequencies, respectively) are more stable vegetated units and more likely to experience sediment deposition than erosion after inundation. For example, only catastrophic or appropriately large or repeated floods are likely to destroy vegetated benches and effectively release seeds from the seed bank (Hupp and Rinaldi, 2007; Erskine et al., 2009). Densely vegetated floodplains are less likely to experience extensive erosion during such events (Beeson and Doyle, 1995).

5.2. Indirect hydrological and fluvial influences on riparian seed banks

Beyond the direct deposition and erosion of sediment and seeds, geomorphology and related hydrological conditions will *indirectly* change the spatial composition of riparian seed banks by mediating seed mortality and germination and by influencing seed inputs to the seed bank by affecting seedling survival and establishment. The effects of variations in flood frequency, inundation duration, and fluvial processes are clearly observable at the geomorphic unit scale through vegetation assemblages (Hupp and Osterkamp, 1985, 1996; van Coller et al., 2000). Bar sediments, positioned close to base flow may be saturated for extended periods. These conditions may favour seed persistence in some wetland and riparian species, whilst increasing rates of seed mortality in more terrestrial species (Bekker et al., 1998). Flows with the capacity to rework the noncohesive sediments may also trigger germination from bar seed banks by exposing them to germination cues such as light and water. Seed mortality and germination result in losses from the seed bank (Fig. 6). Sediment saturation, or conversely, decreased plant water availability associated with coarse bar sediments and the lack of organic matter and nutrients are pressures affecting the survival of seedlings to reproductive maturity with the capacity to contribute seeds to the seed bank (McBride and Strahan, 1984; Naiman and Decamps, 1997; Tabacchi et al., 1998). Typically, a limited array of primarily semiaquatic and/or pioneer species, often capable of prolific seed production, are more likely to survive to reproductive maturity (e.g. *Isolepis* and *Juncus* species; Bossuyt and Honnay, 2008; O'Donnell et al., in press). The net result of these processes operating on bars is likely to contribute to our observations of highly variable seed bank abundance and low species richness.

Benches and floodplains are more stable than bars, owing to their higher elevation and reduced inundation frequency, and support more diverse plant assemblages. Some reworking of bench top sediments during inundating flows may expose seeds to germination cues and trigger germination. The survival of seedlings on benches is also likely to be aided by nutrients provided by fine clays and organic particulates deposited in the waning stages of smaller floods (Erskine et al., 2009) (Fig. 6). These conditions make benches habitable for a greater variety of species than those found on bars, including many dispersed by nonfluvial sources (e.g. wind, animals) (O'Donnell et al., in press). Some of these plant species will ultimately contribute seeds to the seed bank. On the floodplain, less frequent inundation results in infrequent sediment (and seed) deposition, limiting the relative role of fluvial contributions to the seed bank. At the same time, floodplains generally support dense later-successional vegetation assemblages, which have an immense capacity to contribute seeds and organic material to seed banks (Corenblit et al., 2009; O'Donnell et al., in press). Seeds buried during rare fluvial deposition events are, over time, increasingly less likely to be exposed to germination cues as a result of the stability of root-bound floodplain soils and sediment and the infrequency of fluvial disturbance.

5.3. Nonfluvial seed contributions to riparian seed banks

Nonfluvial seed contributions refer to seeds delivered to riparian seed banks via dispersal mechanisms including wind, animals (including mammals, invertebrates, birds, etc.), and direct seed fall from parent plants. This includes nonfluvially dispersed seeds from the aforementioned plants originating from the seed bank, as well as from plants outside the direct influence of fluvial processes such as hillslope and terrace vegetation. Seeds have the capacity to disperse beyond their parent plant, and undoubtedly some seeds from dense floodplain vegetation for example will disperse throughout the riparian zone. Relative contributions of seeds from fluvial and nonfluvial sources will

differ depending on the frequency of inundation and reworking of the geomorphic unit. Ultimately, however, direct seed inputs from the increasingly dense and species-rich vegetation that is commonly observed from the channel bed to the floodplain (Hupp and Rinaldi, 2007; O'Donnell et al., in press) should contribute to the same pattern of increasing seed bank abundance and species richness predicted to result from fluvial processes.

6. Conclusions

A common aim of seed bank research is to determine the potential of the seed bank to contribute to the natural regeneration of vegetation after some management activity (e.g. invasive species removal, water regime change) or natural event (e.g. flood) (e.g. Hughes and Cass, 1997; Crosslé and Brock, 2002; Middleton, 2003; Robertson and James, 2007; Vosse et al., 2008; Cui et al., 2013; O'Donnell et al., in press). Seed bank assays, commonly derived through soil/sediment sampling and seedling emergence studies, help land managers assess strengths and limitations of the seed bank to aid in revegetation (e.g. whether the seed bank holds desirable or invasive species, or later-successional shrubs and trees). Such information can guide expectations of what management actions may need to be applied in the wake of vegetation regeneration (e.g. invasive species removal or tree planting). For this, comprehensive estimates of seed bank abundance and species richness are key. This research suggests that simple observable sedimentological qualities related to organic matter content and particle size may be quite useful for distinguishing between areas of high and low seed bank species richness within a river reach. Finer sediments and those containing high organic matter such as that associated with floodplains and flood debris should be targeted for sampling. Estimations of seed bank abundance are likely to be more challenging, considering seed banks generally show high spatial variability. Nevertheless, the results of this and other studies do point toward slightly higher seed bank abundance in finer sediments than coarser sediments such as sand and gravels. Frequently inundated sediments such as those comprising bars are much more conducive to seed losses and were highlighted as being particularly species poor, making them a poor choice for seed bank sampling. Sediment sampling following these recommendations should elicit useful estimations of seed bank composition.

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Chapter 4

Riparian seed banks and biogeomorphic succession

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CAN THE REGENERATION OF VEGETATION FROM RIPARIAN SEED BANKS SUPPORT BIOGEOMORPHIC SUCCESSION AND THE GEOMORPHIC RECOVERY OF DEGRADED RIVER CHANNELS?

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ABSTRACT

For rivers degraded by erosion and channel widening, the re-establishment of riparian vegetation is essential. We assess the potential for riparian seed banks to facilitate natural channel contraction through the regeneration of plants involved in the biogeomorphic succession of three discrete geomorphic units of increasing age and height above the channel bed: bars, benches and floodplain. Standing vegetation upon each unit type was surveyed for four river reaches in the Hunter catchment of eastern Australia. Seed bank composition was determined using seedling emergence techniques on sediment sampled from the units. We compared species richness and composition, and longevity, growth form and seed dispersal mechanisms between the standing vegetation and seed bank species. The seed bank was similar across bars, benches and floodplain, containing mostly perennial pioneer herbs, sedges and rushes, dispersed by wind and hydrochory (water transport). While bar vegetation was similar to the seed bank, bench and floodplain vegetation included later successional species such as shrubs and trees, significantly more grasses and vines (benches: $\chi^2_{5,\ N=402} = 102.033$, $p < 0.001$; floodplain: $\chi^2_{5,\ N=792} = 30.324$, $p < 0.001$) and higher proportions of unassisted and animal-dispersed seeds (benches: $\chi^2_{5,\ N=352} = 89.409$, $p < 0.001$; floodplain: $\chi^2_{5,\ N=338} = 56.026$, $p < 0.001$). The results suggest that seed banks may support early stages of biogeomorphic succession, via regeneration of pioneer plants. However, plants, such as shrubs and trees that are observed upon units of increasing age and height above the channel bed (i.e. benches and floodplain), are likely sourced from transient seeds produced by local vegetation, rather than seed banks. Copyright © 2014 John Wiley & Sons, Ltd.

KEY WORDS: propagule; geomorphic unit; seed bank; vegetation; biogeomorphic succession

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INTRODUCTION

Riparian vegetation provides important habitat and is a critical influence on ecological and geomorphological processes (Naiman and Decamps, 1997; Corenblit *et al.*, 2008). Consequently, the re-establishment of riparian vegetation has become a major focus of international riparian management strategies and river restoration efforts (Bernhardt *et al.*, 2005; Brooks and Lake, 2007). The re-establishment of vegetation in degraded ecosystems can improve both the ecological and geomorphological integrity of rivers and streams by increasing habitat quality and heterogeneity, as well as reducing erosion through the capture and stabilization of sediment (Rutherfurd *et al.*, 2000; Erskine *et al.*, 2009).

Over the last two decades, there has been increasing interest in using naturally occurring soil and sediment seed banks as a seed source for the revegetation of degraded ecosystems (e.g. Goodson *et al.*, 2001; Middleton, 2003; Richter and Stromberg, 2005; Jensen *et al.*, 2008; Vosse *et al.*, 2008). Supporting natural regeneration from the seed bank, most commonly by changing disturbance regimes, is an example of a passive restoration approach (Kauffman *et al.*, 1997). For example, restricting livestock access to riparian corridors by fencing can improve the integrity of riparian habitat and increase the likelihood of survival for plants regenerating from the seed bank (Rutherfurd *et al.*, 2000). Changing hydrological regimes via water regulation can also favour seed deposition and the establishment of particular suites of species (Merritt and Wohl, 2006; Greet *et al.*, 2012). The removal of dominant weeds or undesirable species can facilitate regeneration of more desirable species residing in the seed bank and in particularly depauperate sites, the direct application of soil/sediment collected from nearby reaches with known abundant seed banks may also be an option (Valk *et al.*, 1992; Nishihiro *et al.*, 2006). The success of any of these approaches hinges on numerous factors, however it is important that the seed bank is both abundant and known to contain a diverse array of species that are appropriate for the range of environmental conditions common to the site.

How likely is it that riparian seed banks are important contributors to the regeneration of diverse riparian vegetation communities? Some studies have shown that there is

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little overlap between the species composition of standing vegetation and seed bank communities in riparian systems (e.g. Beismann *et al.*, 1996; Hughes and Cass, 1997). Other studies suggest that seed banks are generally dominated by early successional species such as herbs, sedges and rushes that are adapted to conditions mediated by frequent disturbance. If this is so, seed banks may lack the functional diversity to restore complex and diverse vegetation communities (Hopfensperger, 2007; Bossuyt and Honnay, 2008). In contrast, other studies have shown that riparian seed banks may contain a wide range of growth forms and tolerances (e.g. Tabacchi *et al.*, 2005; Capon and Brock, 2006). Importantly, seed banks may also contain a large number of seeds of exotic species that may thrive under changed disturbance regimes (Tabacchi *et al.*, 2005).

Most riparian seed bank research has focussed on similarities with the standing vegetation in floodplain environments, where later successional species such as trees and other dominant species are often lacking in the seed bank (e.g. Finlayson *et al.*, 1990; Brock and Rogers, 1998; Capon and Brock, 2006; Webb *et al.*, 2006; Capon, 2007; Jensen *et al.*, 2008; Reid and Capon, 2011). Fewer studies have assessed the composition of within-channel geomorphic features, which are increasingly the focus for restoration activities aimed at arresting bank erosion and enhancing contraction in previously over-widened channels. However, river channel beds and banks have been found to contain diverse and dynamic seed banks, primarily attributed to seed transport and deposition by flowing water (hydrochory; Goodson *et al.*, 2002; Gurnell *et al.*, 2006; Gurnell *et al.*, 2007).

The geomorphological structure of riparian systems provides a useful template for examining seed bank composition and setting goals for the regeneration of vegetation and restoration of riverine habitats (Brierley and Fryirs, 2008). Distinct vegetation communities are often associated with different geomorphic units, as the range of hydrological and fluvial processes that form the units exert differential and selective pressures on species establishment (Kyle and Leishman, 2009). The result is a patch mosaic of different plant assemblages of varying successional stages (Harris, 1987; Richardson *et al.*, 2007). Biogeomorphic succession describes the reciprocal interactions between vegetation and geomorphology, whereby pioneer vegetation assemblages are highly influenced by hydrology and geomorphology, and later successional species increasingly exert their own controls on fluvial processes (Corenblit *et al.*, 2007; Corenblit *et al.*, 2008). The interaction between vegetation, hydrology and geomorphology drives the succession of vegetation and the formation/evolution of geomorphic features via feedbacks between changing plant assemblages, changes in sediment cohesion and rates of deposition. Equally, disturbance events with a magnitude and power significant enough to induce changes to the erosion–deposition balance can set vegetation succession back to a previous stage (Corenblit *et al.*, 2007).

This paper aims to assess the potential of the seed bank to facilitate the regeneration of the vegetation communities specific to three discrete geomorphic features, bars, benches and the floodplain, in the Hunter Valley catchment of New South Wales, Australia. Many of the streams in this region experienced extensive erosion and channel widening after a series of floods in the 1940s, as a result of the widespread clearance of riparian vegetation (King and Woolmington, 1960; Webb and Erskine, 2003; Fryirs *et al.*, 2012). As such, restoration and management strategies include enhancing vegetation growth to encourage sediment deposition, stabilization and channel contraction (Schneider, 2007). We compare the composition of the seed bank with the standing vegetation to assess the degree to which the seed bank may provide those species currently involved in biogeomorphic succession and channel contraction processes. Specifically we asked the following questions:

1. How does the species richness and composition of the seed bank compare with the standing vegetation on bars, benches and the floodplain?
2. Are the functional traits of the species in the seed banks of bars, benches and the floodplain different from those of the standing vegetation?
3. Of what origin and what growth forms are the most abundant species in the seed bank?
4. Are species targeted for revegetation in the region present in the seed bank?

METHODS

Study sites

This study was conducted along four stream reaches in the Wollombi Brook subcatchment in the lower Hunter River catchment of New South Wales, Australia (Figure 1). The Wollombi subcatchment drains an area of 341 km^2. Average annual rainfall since 1903 is approximately 750 mm, and the region experiences average annual maximum and minimum temperatures of 24.6 and 11.1°C. Compared with Australian and world standards, the Hunter Region has a high flash flood magnitude index (Erskine and Saynor, 1996). An upper and mid-reach site was chosen along both Watagan Creek (sites 1 and 2, respectively), a large tributary of Wollombi Brook, and along Wollombi Brook itself (sites 3 and 4, respectively), the main drainage channel for the subcatchment. Significant work on post-European river change and the impacts of historical flooding have previously been conducted in these reaches (Erskine and Melville, 2008; Fryirs *et al.*, 2012). The study reaches selected were the result of a routine search for relatively undisturbed reaches within

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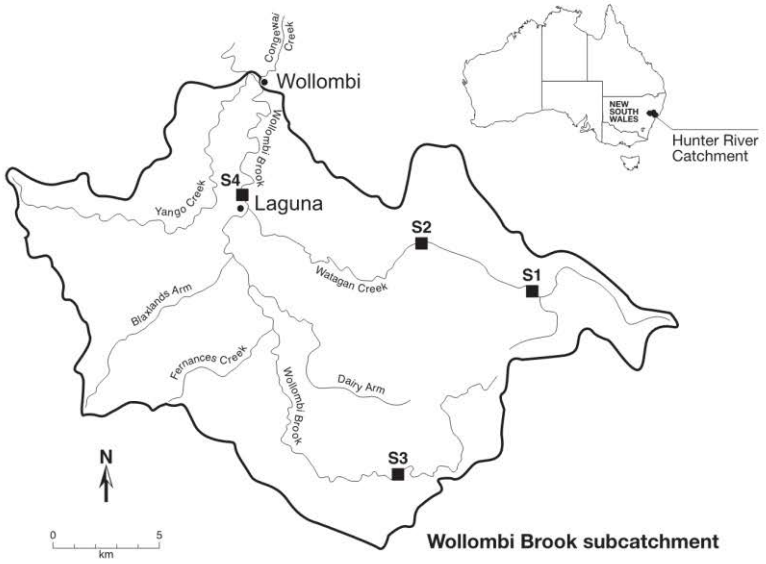

Figure 1. Map showing the location of the four study sites within two reaches of Watagan Creek and two reaches of Wollombi Brook in the Wollombi subcatchment of the lower Hunter River catchment, New South Wales, Australia. Map modified from Erskine and Melville (2008).

the subcatchment, for which we could negotiate access with local landholders. The two upstream sites (1 and 3) are valley-confined sand and gravel bed streams, with occasional pockets of floodplain (Brierley and Fryirs, 2005). Channel bed slope averages 0.0035 m/m (Fryirs *et al*., 2012). Both sites have well-developed assemblages of native vegetation with minimal encroachment of exotic species and are situated either within or adjacent to state forests. The two mid-catchment reaches (2 and 4) are partly confined planform-controlled sand bed streams with discontinuous floodplain pockets (Brierley and Fryirs, 2005). Channel bed slope averages 0.0025 m/m (Fryirs *et al*., 2012). The site 2 reach has well-developed vegetation with moderate weed encroachment. Grazing occurs within the immediate vicinity of the reach. The site 4 reach is lacking a substantial riparian vegetation strip because of clearing of the floodplain and current grazing and viticulture. This reach has moderate weed encroachment.

Seed bank sampling

Samples of soil and sediment were collected from bars, benches and the floodplain along a 100-m reach at each of the four sites. Bars were identified as deposits of non-cohesive, sparsely vegetated sand with maximum elevations ranging from approximately 0.3 to 0.8 m above the channel bed. These features are inundated by the regular low flow condition. Benches are bank-attached, flat-topped depositional structures at higher elevations than bars and common in reaches recovering from historical channel incision and widening. They develop extensive coverings of vegetation over time, which increases sediment cohesion and resistance to erosion by adequate flows. In this system, they tend to be inundated in a 1 in 5-year flow (Fryirs *et al*., 2012). Floodplains across the four sites were situated at elevations up to approximately 4 m above the channel bed. These surfaces are inundated in a 1 in 10-year flow or greater (Fryirs *et al*., 2012). While inundated irregularly, the floodplains are actively forming. Within each study reach, bars and benches were distinguished according to the previously mentioned descriptions, and three discrete bar and bench geomorphic units were chosen for sediment sampling. Sediment was also sampled at three locations on the floodplain between 30 and 50 m apart, parallel to the channel and within 8 m of the bankfull channel edge. From each of the three replicate bars, benches and floodplain areas chosen for sampling at each of the four study reaches, three sediment samples to a depth of 30 cm (some bars were only sampled to 20 cm because of water infiltration), were collected using a trowel from within an area of approximately 1×1 m and pooled. This resulted in a total of 36 sediment samples, each representing a single geomorphic unit replicate. The samples were stored at 4°C before commencing the seedling emergence study between 2 and 12 days later.

Seedling emergence study

To identify the composition of the seed bank within the sediments of the bars, benches and floodplain, a seedling emergence study was conducted at Macquarie University's Plant Growth Facility. Each pooled sample was divided into six 450 cm^3 subsamples that were each spread to a depth of

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approximately 1 cm over 2 cm of washed river sand in four 7 × 13 × 5-cm punnets. The four punnets for each subsample were kept together in a seedling tray with another randomly chosen subsample (i.e. eight punnets per seedling tray). The total number of samples was 203. Six control seedling trays containing sand only were also placed within the glasshouse, to confirm the absence of seeds in the sand and to detect species possibly originating from seeds or spores entering the glasshouse from outside. The seedling trays were randomly allocated a position within the glasshouse and were randomly repositioned several times throughout the study. Temperatures within the glasshouse were maintained between 18 and 23°C, and the samples were mist watered as necessary to keep the soil continually moist. The conditions were administered to promote germination across as wide a number of species as possible. Each seedling that emerged was identified to species level, tallied and then removed. Plants that could not be identified were replanted and grown to an age where identification was possible. Taxonomic nomenclature follows Harden (1990, 1991, 1992, and 1993). Upon completion of the study, the species counts for the six subsamples for each geomorphic unit replicate were combined, providing seed bank abundance and species composition for a sample of approximately 2700 cm^3 and representing the seed bank to a depth of 30 cm. The emergence study commenced in May 2011 and ended in January 2012 after no germination was observed in any of the samples for 2 weeks. The seedling emergence method captures the germinable seed bank, that is, those species that readily germinate in response to favourable conditions. This method will fail to detect those species with long-term physical or chemical dormancy and thus presents a conservative estimate of the true potential of the seed bank for the regeneration of vegetation. During the course of the study, several species germinated from spores (i.e. ferns) or regenerated from root or stem fragments. While not technically originating from seeds, we considered all regeneration important and included all species that emerged during the study as components of the greater 'propagule' bank, hereafter referred to as the seed bank.

Survey of standing vegetation

A survey of the standing or aboveground vegetation was conducted along each of the four study reaches during October 2011, with a follow-up survey in April 2013 to capture new species or those missed during the 2011 survey. Within each study reach, the percentage cover of groundcover vegetation including herbs and small shrubs was estimated for bars, benches and the floodplain in six 1 × 1-m quadrats allocated to each geomorphic unit type. For bars and benches, the six quadrats were positioned to sample as many independent units as possible within the 100-m reach. However, benches were often long and few in number, requiring multiple quadrats to be established along their length. At site 1, the total surface area of benches allowed space for only five independent quadrats. At site 3, the bars were inundated at the time of the survey, preventing surveying of this unit type altogether. Some surveyed bars were unvegetated. The six floodplain quadrats were randomly positioned by throwing a marker within an 8-m-wide and 100-m-long transect perpendicular to the channel. Unique understory and canopy species were identified on benches and the floodplain by observation from walking the length of the study reach. Taxonomic nomenclature again conforms to Harden (1990, 1991, 1992, and 1993).

Plant functional trait information

A database of traits was established for all species identified from both the seed bank and the standing vegetation in the study. Species were categorized into taxonomic family, longevity (annual/perennial/biennial), origin (native/exotic) and growth form (grass, herb, shrub/tree, fern, vine/climber, sedge/rush and aquatic). Six seed dispersal categories (human-mediated dispersal was excluded) were also identified for all species, including unassisted dispersal (no obvious dispersal mechanism) by animals (e.g. fleshy fruits, seeds with arils, etc.), hydrochoric dispersal (water mediated), dispersal by wind (e.g. seeds with wings or pappus), and then two commonly combined categories, wind and animals, and wind and hydrochory. Species for which only vegetative fragments were detected in the seed bank were not included in the dispersal analysis. All data were derived from a range of sources including online databases such as PlantNET (Botanic Gardens Trust, 2012), relevant literature and various online sources.

Data analysis

Species richness and composition of the seed bank and standing vegetation. To investigate relationships between the species richness of the seed bank and standing vegetation in relation to the three geomorphic unit types, we employed generalized linear mixed models (GLMMs) based on restricted maximum likelihoods. Three factors were included in the model: site (four levels: sites 1–4), geomorphic unit (three levels: bar, bench and floodplain) and sample (two levels: seed bank and standing vegetation). Geomorphic unit was nested within site for the analysis and site identified as a random factor. The response variable species richness was log10 transformed for normality prior to analysis. Untransformed species richness data for the seed bank and standing vegetation were also compared between units at the reach scale—i.e. the total seed bank or standing vegetation species richness observed for the combined replicates of each geomorphic type within each study reach.

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To compare the species composition of the seed bank samples with that of the standing vegetation survey quadrats, the seed bank abundance data (counts from the seedling emergence experiment) and the standing vegetation data (average percentage cover) were firstly converted to species presence–absence data because of the difference in sampling techniques used. From these data, a Sørensen-derived similarity matrix including all samples was generated. Permutational analysis of variance (PERMANOVA) was used to investigate the influence of, and possible interactions between, sample type (fixed factor, 2 levels: seed bank/standing vegetation) and unit type (fixed factor, 3 levels: bar/bench/floodplain) on species composition. For this analysis, unit type was nested within the factor site (random factor, four levels: sites 1–4). The analysis utilized type III partial sums of squares, permutation of residuals under a reduced model and 999 permutations. Analysis of similarity (ANOSIM), with 1000 permutations (where possible), was then employed to assess the relative species compositional differences between the seed bank and standing vegetation between bars, benches and the floodplain. Non-metric multidimensional scaling (NMDS) was used to visualize the differences. All multivariate analyses were conducted in PRIMER v.6 (Clarke and Warwick, 2001).

Comparison of plant functional traits between the seed bank and standing vegetation. To estimate the extent to which the seed bank captures the diversity and ecological variation of the standing vegetation upon bars, benches and the floodplain, we compared the proportions of species (i) longevity, (ii) growth form and (iii) dispersal mechanisms between the seed bank and standing vegetation using chi-square analysis or Fisher's exact tests where samples sizes were too small for the former. Analyses were conducted in SPSS v.20 (SPSS Inc., 2011). Based on the summed totals for each geomorphic unit type, we tested the null hypothesis of no association between the sample origin (seed bank versus standing vegetation) and the proportional counts of categories within each trait.

Abundant species in the seed bank and species targeted for restoration activities. To examine those species that dominate the seed bank, as opposed to those that occurred rarely, we selected all species with greater than 20 seeds detected in the seedling emergence experiment. Growth form, origin (native versus exotic) and presence in the seed bank and standing vegetation of bars, benches and the floodplain were recorded. Specific species targeted for revegetation efforts in the Wollombi region (as according to Schneider, 2007) that were present in the seed bank were identified.

RESULTS

Species richness

A total of 9456 seedlings emerged from the seeds, spores and vegetative propagules present in the seed bank samples of bars (5134 seedlings), benches (1998 seedlings) and the floodplain (2324 seedlings). The total number of species identified from the seed bank and standing vegetation was 182, representing 55 families. Of these, 73 (40%) species were present only in the seed bank, 54 (30%) species were restricted to the standing vegetation, and 55 (30%) species were present in both. Native species comprised 67% of the seed bank and 70% of the standing vegetation. Sørensen's index of similarity (Sørensen, 1948) between the species observed in the seed bank and the standing vegetation was 47.458.

The average species richness of the seed bank detected across the sampled bars, benches and floodplain within a study reach (i.e. reach scale) was 26.5 9.1, 39 7, and 44 8.8, respectively, with averages per individual sample being 12.1 6.2, 21.9 7.4, and 24.1 7.6, respectively (Figure 2). Species richness of the standing vegetation at the reach scale for bars, benches and floodplain was 10.2 9.1, 20.7 6.7, and 26.2 8.8, respectively, with

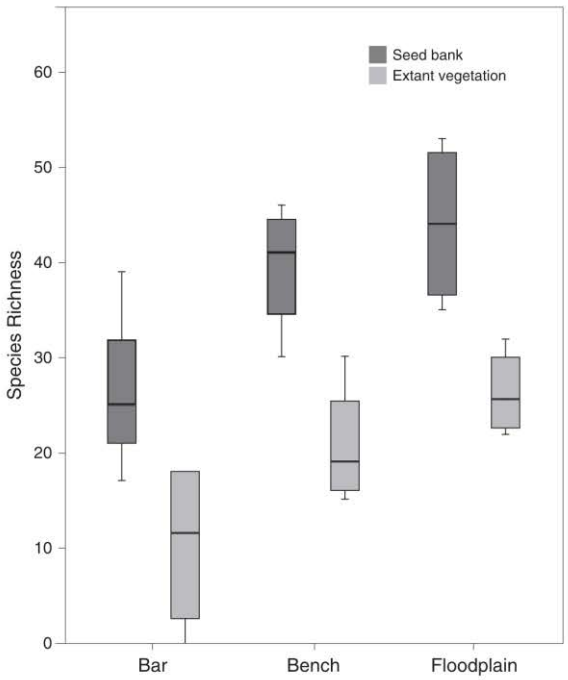

Figure 2. Boxplot showing species richness of the seed bank and standing vegetation observed for bars, benches and the floodplain at the reach scale. Error bars represent 95% confidence intervals around the median across the four sites.

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averages for individual survey plots being 4.4 2.4, 5.8 3.2, and 9.5 3.9, respectively (Figure 2).

At the sample scale, a significant interaction between sample type (i.e. seed bank versus standing vegetation) and geomorphic unit type (nested within site) was found to affect species richness (GLMM, $F_{10,\ 73} = 2.337$, $p = 0.019$). This interaction was not apparent at the reach scale. Species richness was consistently higher in the seed bank samples than the standing vegetation survey quadrats at both the sample scale (GLMM, $F_{10,\ 73} = 120.081$, $p < 0.001$) and reach scale ($F_{1,\ 18} = 30.910$, $p < 0.001$; Figure 2). Overall species richness (seed bank and standing vegetation) increased significantly from bars to benches and then floodplain at the sample scale (GLMM, $F_{8,\ 73} = 9.038$, $p < 0.001$). At the reach scale, the species richness of bars was significantly lower than benches and the floodplain (GLMM, $F_{2,\ 18} = 9.856$, $p = 0.001$; Figure 2). Weakly significant site-based differences were detectable at the sample scale (GLMM, $F_{1,\ 73} = 3.087$, $p = 0.032$).

Species composition

The ordination produced by NMDS of the Sørensen similarity matrix data indicates that the species composition of the seed bank samples was generally much less variable than that of the standing vegetation survey quadrats (Figure 3). The stress value of 1.6 suggests that some distances within the ordination may not fully represent the similarity between the samples. The PERMANOVA analysis revealed a significant interaction between the geomorphic unit type (which was nested within site) and the sample type ($F_{7,73} = 2.3082$, $p = 0.001$), suggesting that the compositional difference between the seed bank and standing vegetation differed between bars, benches and the floodplain. When analysed separately using ANOSIM, the species composition of the seed bank was significantly different to that of the standing vegetation for each geomorphic unit type (bars: $R = 0.152$, $p = 0.013$; benches: $R = 0.494$, $p = 0.001$; floodplain: $R = 0.469$, $p = 0.001$). Bars, however, showed greater similarity in species composition between the seed bank and standing vegetation. The standing vegetation on bars was significantly different to that of benches ($R = 0.427$, $p = 0.001$) and the floodplain ($R = 0.507$, $p = 0.001$), but benches and the floodplain had similar assemblages. In contrast, the seed bank composition of bars and benches was only mildly significantly different ($R = 0.097$, $p = 0.046$) but significantly different between bars and floodplain ($R = 0.373$, $p = 0.001$), and bench and floodplain ($R = 0.219$, $p = 0.009$).

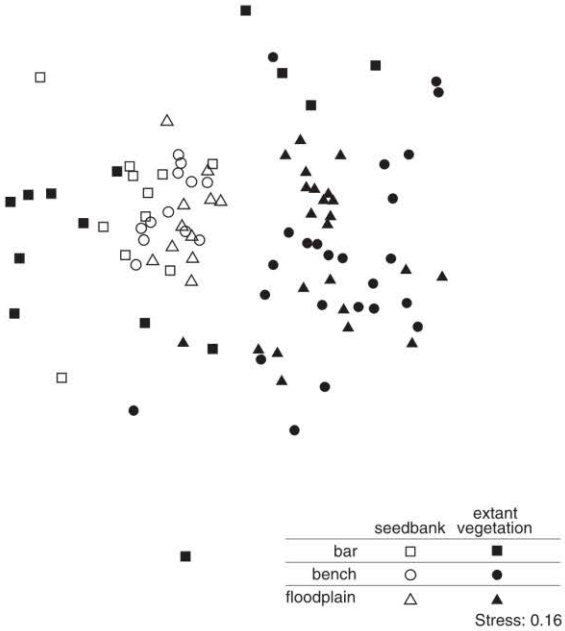

Figure 3. Ordination based on non-metric multidimensional scaling (NMDS) of Sørensen-derived similarities of species composition (based on the presence or absence), for the individual seed bank samples and standing vegetation survey quadrats, for bars, benches and the floodplain across the four sites.

Functional traits of the seed bank and standing vegetation: plant longevity, growth form and seed dispersal mechanisms

Perennial species dominated both the seed bank and standing vegetation (Figure 4). For bars, there was no significant

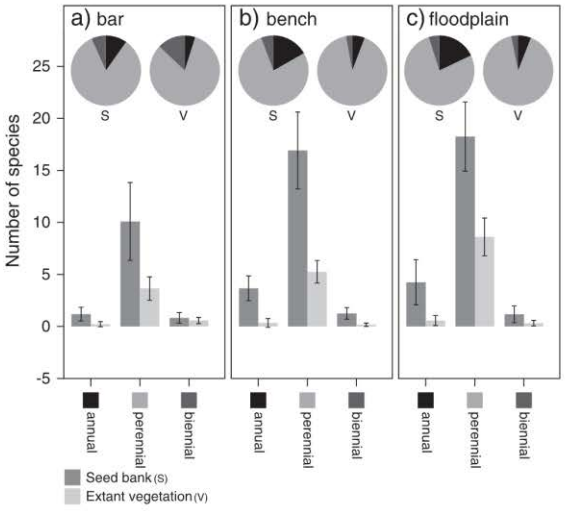

Figure 4. Average number of annual, perennial and biennial species in seed bank samples (dark grey) and standing vegetation survey quadrats (light grey) for (a) bars, (b) benches and (c) floodplain, across the four study sites. Error bars represent 95% confidence intervals. Embedded pie charts show the relative proportions of each longevity category compared between the seed bank and standing vegetation for each geomorphic unit.

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difference between the seed bank and standing vegetation in the proportion of longevity classes. On the benches and floodplain, the seed bank contained relatively more annuals than the standing vegetation (Fisher's exact test, benches: $p = 0.002$; floodplain: $p < 0.001$; Figure 4).

The proportion of different growth forms did not differ between the seed bank and standing vegetation for bars. In both, herbs, sedges and rushes accounted for approximately 77% of species. In both benches and the floodplain, however, the growth form proportions differed significantly (benches: $\chi^2_{5,\ N=402} = 102.033$, $p < 0.001$; floodplain: $\chi^2_{5,\ N=792} = 30.324$, $p < 0.001$). For both geomorphic units, the proportions of sedges and rushes were higher, and the proportions of both grasses and vines were lower in the seed bank compared with the standing vegetation. On benches and the floodplain, grasses and herbs dominated the standing vegetation, accounting for 67 and 70% of species, respectively (Figure 5).

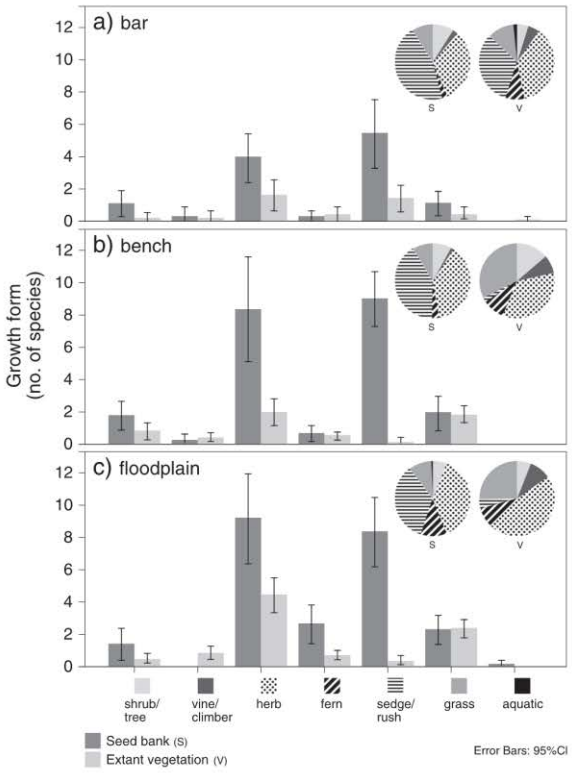

Figure 5. Average number of species representing seven growth-form types in seed bank samples (dark grey) and standing vegetation survey quadrats (light grey) for (a) bars, (b) benches and (c) floodplain, across the four study sites. Error bars represent 95% confidence intervals. Embedded pie charts show the relative proportions of each growth form category for the seed bank and standing vegetation for each geomorphic unit.

The seed bank of all three geomorphic units tended to be dominated by species dispersed via hydrochory, wind, or a combination of the two (Figure 6). In bars, the standing vegetation had a greater proportion of species with no identified dispersal mechanism (unassisted; Fisher's exact test, $p = 0.003$). On benches and the floodplain, the standing vegetation had greater proportions of unassisted and animal-dispersed seeds (benches: $\chi^2_{5,\ N=352} = 89.409$, $p < 0.001$; floodplain: $\chi^2_{5,\ N=338} = 56.026$, $p < 0.001$; Figure 6).

Abundant species in the seed bank

Of the 129 species detected in the seed bank, fewer than 20 seeds were detected for 94 species. Across the four study reaches, 83 and 66 species had fewer than 10 and 5 seeds detected, respectively. Of the 35 species for which more than 20 seeds were detected, seed counts ranged between 3480 and 20 seeds (Table 1). Of these, herbs (15 species and 3739 seeds) and sedges and rushes (12 species and 4803

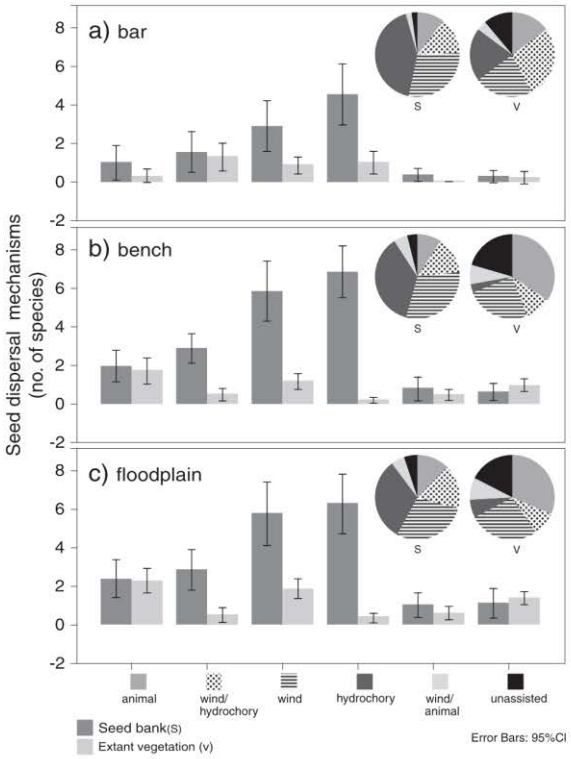

Figure 6. Average number of species displaying six different seed dispersal mechanism categories in seed bank samples (dark grey) and standing vegetation survey quadrats (light grey) for (a) bars, (b) benches and (c) floodplain, across the four study sites. Error bars represent 95% confidence intervals. Embedded pie charts show the relative proportions of each seed dispersal mechanism category for the seed bank and standing vegetation for each geomorphic unit.

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Table I. List of species for which 20 or more seeds were detected in the seed bank, presented in order of number of seeds detected in the seedling emergence study (seed count) and growth form

			Sites present in seed bank			Present in standing vegetation		
Seed count	Species	Growth form	Bar	Bench	Floodplain	Bar	Bench	Floodplain
3480	*Isolepis inundata*	SR	Y	Y	Y	Y		
2795	*Gratiola peruviana*	H	Y	Y				
345	*Juncus continuus*	SR	Y	Y	Y			
244	*Conyza sumatrensis*[a]	H	Y	Y	Y	Y	Y	Y
179	*Juncus cognatus*[a]	SR	Y	Y	Y			
168	*Juncus planifolius*	SR	Y	Y	Y	Y		
158	*Juncus articulatus*[a]	SR	Y	Y	Y			
144	*Oplismenus aemulus*	G	Y	Y	Y	Y	Y	Y
122	*Juncus prismatocarpus*	SR	Y	Y	Y	Y		
121	*Verbena bonariensis*[a]	H		Y	Y		Y	Y
115	*Juncus microcephalus*[a]	SR	Y	Y	Y	Y	Y	
97	*Callicoma serratifolia*	ST	Y	Y	Y			
97	*Calochlaena dubia*	F	Y	Y	Y			Y
95	*Gamochaeta calviceps*[a]	H	Y	Y	Y			
87	*Gamochaeta americana*[a]	H	Y	Y	Y			Y
82	*Juncus capillaceus*[a]	SR	Y	Y	Y			Y
81	*Hydrocotyle peduncularis*	H	Y	Y	Y		Y	Y
72	*Viola hederacea*	H	Y	Y	Y	Y		
54	*Cyperus sesquiflorus*[a]	SR		Y	Y			
46	*Oxalis perennans*	H	Y	Y	Y		Y	Y
45	*Cyperus laevis*	SR	Y	Y	Y			
44	*Digitaria ciliaris*[a]	G	Y	Y	Y			
41	*Hydrocotyle tripartita*	H	Y	Y			Y	Y
39	*Persicaria lapathifolia*	H	Y	Y		Y		
32	*Setaria parviflora*[a]	G	Y	Y	Y			Y
28	*Isolepis prolifera*[a]	SR	Y	Y	Y			
27	*Axonopus fissifolius*[a]	G	Y	Y			Y	Y
27	*Centipeda minima*	H	Y	Y				
27	*Ficus coronata*[c]	ST	Y	Y	Y	Y	Y	
27	*Lepidosperma limicola*	SR	Y	Y	Y			
26	*Davallia solida var. pyxidata*	F	Y	Y	Y	Y		
25	*Tradescantia fluminensis*[ab]	H	Y	Y	Y	Y	Y	Y
23	*Cerastium glomeratuma*[a]	H		Y	Y			
23	*Veronica plebeia*	H		Y	Y			Y
20	*zcp*	H	Y		Y			Y

F, fern; G, grass; H, herb; ST, shrub/tree; SR, sedge/rush. Y indicates present in seed bank or standing vegetation for bars, benches and floodplain.
[a]Exotic species.
[b]Species regenerating from root fragments.
[c]Species targeted for revegetation in region.

seeds) dominated. The remaining species were grasses (4 species and 247 seeds), ferns (2 species and 123 spores) and shrub/trees (2 species and 124 seeds). Fifteen of the species with the most abundant seed banks were exotic, including seven herbs, seven sedges or rushes and three grasses. Thirteen of the seed bank species were not observed in the standing vegetation at all, and the majority of species were not always recorded in the standing vegetation upon the units for which seed banks were detected.

Target species for revegetation activities in the seed bank

Four species targeted for revegetation activities within the region were detected in the seed bank including the tree *Ficus coronata* (27 seeds), grass *Microlaena stipoides* (stem and root fragments), rush *Juncus usitatus* (1 seed) and the tussocky herb *Lomandra longifolia* (2 seeds; Schneider, 2007). Two seeds of the vine *Cissus hypoglauca*, closely related to the target species *Cissus antarctica*, were also detected.

DISCUSSION

We examined the potential of the seed bank as a regeneration source for plant species involved in biogeomorphic succession on discrete bars, benches and the floodplain of streams in the lower Hunter catchment of eastern Australia. Firstly, we asked how the species richness and composition

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of the seed bank compare with the standing vegetation and found that the seed bank displayed higher species diversity but differed in composition to the standing vegetation upon all units. Secondly, we asked how the species composition of the seed bank in bars, benches and the floodplain differ from the standing vegetation in relation to species longevity, plant growth form and mechanisms for seed dispersal. We found that the seed bank of bars was most similar to the standing vegetation of bars where perennial sedges, rushes and herbs were the dominant growth form, and wind and hydrochory were the primary dispersal mechanisms. Conversely, bench and floodplain seed banks housed more sedges and rushes and lower proportions of terrestrial plants such as grasses and climbers than observed in the standing vegetation. Furthermore, the standing vegetation on these units was dominated by species with unassisted, wind-dispersed and animal-dispersed seeds, suggesting significant recruitment from surrounding vegetation, rather than river flows. Thirdly, we asked which growth forms and species origin dominate the seed bank and found that pioneer herbs, sedges and rushes, including several exotic species, were most abundant. Finally, we detected the presence of four species currently targeted for revegetation efforts in the region.

Overall compositional differences between the seed bank and standing vegetation

Overall, the seed bank contained 30% of the species that were found in the standing vegetation across the four reaches. This is comparable with the findings of Beismann (1996) and Hughes and Cass (1997). Sørensen's index of similarity was 47.458, equal to the average value for wetlands (review by Hopfensperger, 2007) but considerably higher than values found for other streams (Goodson *et al*., 2002; Vosse *et al*., 2008). Consistent with Vosse *et al*. (2008) but contrary to the findings of Goodson *et al*. (2002), species richness of the seed bank was greater than the standing vegetation for all three geomorphic units, across the majority of growth forms (Figures 2 and 6). This likely reflects supplementation of local seed inputs by the seasonally variable deposition of hydrochoric propagules from upstream vegetation (Jansson *et al*., 2005; Vogt *et al*., 2006). Seed bank diversity may be further increased over successive deposition events because of variability in seed travel distances and burial depth under different flow regimes and discharges (Goodson *et al*., 2003; O'Donnell *et al*., 2014).

While species richness of the seed bank was high, its compositional variability across the samples was lower than that found in the standing vegetation (Figure 3), a phenomenon common across a range of different environments (Hanlon *et al*., 1998; Webb *et al*., 2006; Bossuyt and Honnay, 2008; Corenblit *et al*., 2009). The variability observed in the standing vegetation is typical of the patch dynamics observed within riparian ecosystems (Pringle *et al*., 1988). Spatial differences in seed germination and seedling survival occur because of abiotic factors such as inundation, sediment deposition and nutrient concentration, as well as the influence of these on biotic factors such as seed inputs and competition (Bornette *et al*., 2008; Corenblit *et al*., 2009). At the reach scale, diversity is further increased as disturbances reset plant succession at varying frequencies across different geomorphic features and patches (Ward *et al*., 2002). Of importance to note is that these same factors that have historically operated to determine current plant assemblages will also affect the survival and establishment of seeds germinating from the seed bank.

Plant functional traits and potential for riparian seed banks to support biogeomorphic succession of bars, benches and floodplain

Bars. Rush and sedge species such as *Juncus* (Juncaeae) and *Isolepis* (Cyperaceae) were most common on bars. These species tolerate inundation through physiological adaptations that allow gas exchange during submergence, and their dominance in the standing vegetation indicates that inundation is still a major controlling factor for plant establishment on bars (Blom *et al*., 1994; Naiman and Decamps, 1997). The presence of sedges and rushes, however, can serve to increase the stability and vertical development of bars. For example, their presence can increase the roughness of channel margins thereby reducing the shear stress and velocity of flows at channel margins (Brooks and Brierley, 2002). Perennial species may further increase the stabilization of sediment through denser root stock development. Increased sediment cohesion favours deposition over erosion, resulting in sediment accumulation at the channel margin and thus a reduction in inundation frequency. This may facilitate the establishment of more terrestrial species that favour lower levels of disturbance and inundation (Hupp and Osterkamp, 1996).

The high similarity between the seed bank and standing vegetation of bars (Figures 3 and 5) is likely to reflect the importance of regeneration from the seed bank in determining vegetation composition after disturbances such as flooding and erosion (Gurnell *et al*., 2006). The high abundance of inundation-tolerant sedges and rushes in the seed bank (Figure 5), is strongly suited to bar environments. No dominant growth forms found in the standing vegetation were lacking from the seed bank, suggesting the potential for the establishment of later successional species. However, some specific species observed in the standing vegetation were not detected in the seed bank. Greater than 75% of the seed bank species were water dispersed and wind dispersed, suggesting the potential for bar seed banks to capture additional diversity from upstream and local vegetation assemblages (Gurnell *et al*., 2008). Unassisted and animal-dispersed seeds were

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more common in the standing vegetation, suggesting the importance of these dispersal mechanisms for transient-seeded local species.

Benches. Perennial herbs, grasses and shrubs dominated the standing vegetation on benches (Figures 4b and 5b), displaying a distinct shift away from the inundation-tolerant assemblages most common on bars. ANOSIM based on Sørensen similarities revealed bench vegetation to be much more similar to that of the floodplain, likely reflecting the reduced influence of inundation on these higher elevation landforms (Harris, 1987; Harden, 1993; Tabacchi *et al.*, 1998; Nicol *et al.*, 2003). The structural support of bench development is particularly important in streams where erosion and channel widening or incision have caused disconnection between the channel and floodplain (Hupp and Simon, 1991; Fryirs and Brierley, 2001). Later stages of bench development can function as an 'inset' floodplain (Thoms and Olley, 2004). The establishment of perennial species, especially shrubs and trees, should facilitate the greatest sediment capture of all the growth forms and thus continue to support bench development and channel contraction (Corenblit *et al.*, 2009). For example, we observed scattered seedlings of shrubby trees such as *Myrsine howittiana* and *Rhodomyrtus psidioides,* as well as the large tree *Tristaniopsis laurina* on benches.

The seed bank of benches was compositionally different to that observed in the standing vegetation, questioning the role that seed banks may play in the regeneration of bench plant communities. The seed bank contained much lower proportions of grasses, shrubs, trees and vines than the standing vegetation (Figure 5b). The dominance of water-dispersed sedge, rush and herb species suggests the still persistent influence of hydrochory on the formation of bench seed banks, even at their raised elevation (Figure 6b; Goodson *et al.*, 2003; Moggridge *et al.*, 2009). In contrast, many of the species established on the benches had unassisted dispersal and animal-mediated or wind-mediated dispersal, suggesting substantial recruitment from nearby vegetation. No detectable seed bank was found in benches for five out of six of the most common shrub and tree species found across the sites. Similar results were found for vines, and grass diversity was much higher in the standing vegetation (Table 1; Figure 5b). Revegetation goals for benches typically involve the planting of shrubs and trees, which are effective at stabilizing sediment and promoting deposition (Webb and Erskine, 2003; Erskine *et al.*, 2009). As the abundance of these species in the seed bank was low, the potential for regeneration from the seed bank to drive biogeomorphic succession beyond the levels provided by herb, sedge and rush cover may be limited and instead may depend on the availability of seed from nearby vegetation.

Floodplain. The species richness and taxonomic diversity of the floodplain vegetation were the greatest of the three geomorphic units and the least spatially variable (Figures 3 and 4c). This may reflect the elevation of the floodplain and thus reduced disturbance associated with inundation, erosion and deposition. Perennial herbs comprised nearly 50% of species, and grasses made up a further 25% (Figures 4c and 5c). Surprisingly, shrub and tree diversity was lower than that found on benches; however, the small understory trees *Neolitsea dealbata* and *Abrophyllum ornans* were observed only on the floodplain. Established trees can protect the floodplain from erosion during large floods (Corenblit *et al.*, 2009). They also maximize the diversity of native plant species, provide habitat for organisms, increase the resistance of the community to invasion by exotic species, and provide a source of seed for the regeneration of vegetation after disturbance (Webb and Erskine, 2003; Corenblit *et al.*, 2009). The high diversity of herbs, vines, ferns and grasses (Figure 5) found on the floodplain contributes to these functions.

The floodplain seed bank was taxonomically more diverse than that found for bars and benches but was still significantly different in composition to the standing vegetation (Figure 3). Of the large number of hydrochorically dispersed sedges and rushes present in the seed bank, few were present in the standing vegetation (Figures 5c and 6c) suggesting inappropriate conditions for their establishment. Again, the dominance of unassisted or animal-dispersed seed species in the floodplain vegetation suggests that recruitment from immediate and nearby vegetation is likely to be a more important mechanism for increasing species diversity (Goodson *et al.*, 2003). Very few shrub and tree species were detected in the seed bank; however, some may have been missed because of seed dormancy and failure to germinate under the glasshouse conditions (Cochrane *et al.*, 2002). Similarly, many tree species, including locally dominant later successional *Eucalyptus* species, generally produce transient seeds and do not form seed banks (Webb and Erskine, 2003).

Abundant species within the seed bank

While the seed bank displayed higher levels of diversity than the standing vegetation, examination of the most abundant species in the seed bank (Table 1) highlights some limitations for use in revegetation efforts. Firstly, the high abundance of herb, sedge and rush species in the seed bank (Table 1) is typical of these species adapted to disturbance (Baskin and Baskin, 1998; Thompson *et al.*, 1998). As such, regeneration from the seed bank may be most suited to secondary succession after disturbance events such as flood scouring or deposition (Bossuyt and Honnay, 2008). Secondly, several abundant species were exotic (Table 1),

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which is typical of many riparian areas, especially those influenced by human activity (e.g. King and Buckney, 2001; Cockel and Gurnell, 2012). The majority of exotics that we detected were non-noxious grasses, herbs and sedges. However, some invasive exotic species can be quick to take advantage of the spaces opened by disturbances and may produce prolific numbers of persistent seeds that are easily transported through riparian corridors (Battaglia, 1996; Holmes *et al*., 2005; Richardson *et al*., 2007). As such, assessment of the presence of exotic or invasive species in the seed bank through methods such as seedling emergence studies, prior to management activities that support regeneration from the seed bank, is very useful.

Of 37 plant species identified by Schneider (2007) as key riparian species for revegetation activities in the region (Wollombi), the only species for which we detected a considerable seed bank was the shrubby tree *F. coronata* (Table 1), which is planted along banks to aid stabilization. However, three other target species and one close relative were identified amongst those species with less abundant seed banks. These were the grass *M. stipoides* (and some root/stem fragments), rush *J. usitatus*, tussocky herb *L. longifolia* and vine *C. antarctica*, respectively. Low seed counts may reflect the high diversity but low abundance of individual species' seeds delivered by floods (Tabacchi *et al*., 2005). Sparse seed banks, as particularly observed for later successional species, may decrease the likelihood of successful germination and establishment of these target species. However, it is likely that some of the dominant tree genera in the region (e.g. *Eucalyptus*, *Casuarina* and *Acacia*) rely more on transient seed banks and/or seed release coincident with hydrological regimes to maximize the likelihood of germination and subsequent seedling survival (Thompson and Grime, 1979; Pettit and Froend, 2001). Ultimately, supplementary planting of desirable species that fail to establish for whatever reason may be required to achieve restoration goals.

CONCLUSION

The findings of this study highlight the advantages and disadvantages of using seed bank germination in riparian revegetation practice. Dominance by pioneer species and the significant presence of exotic species suggest the potential to provide for initial regeneration of vegetation on unvegetated surfaces, such as recent sediment deposits, or flood-scoured features. However, the seed bank is likely to be insufficient to provide recruitment for the diverse later successional native vegetation assemblages observed on benches and the floodplain. Monitoring regeneration from the seed bank, and actions such as the selective removal of undesirable species would be essential to make the most from seed bank-based vegetation re-establishment. The results of this study further suggest that with the exception of depositional bars, much of the recruitment for the vegetation assemblages along and within the river channel is from transient seeds produced by standing vegetation, rather than the seed bank. This highlights the great importance of remnant vegetation as a source for recruitment in riparian ecosystems.

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Chapter 5

Seed banks in relation to riparian condition

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Seed banks as a source of vegetation regeneration to support the recovery of degraded rivers: A comparison of river reaches of varying condition

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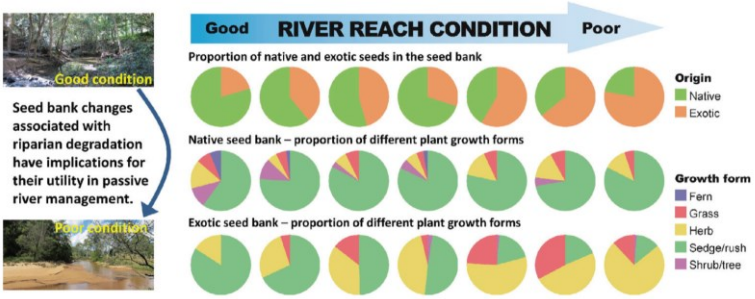
HIGHLIGHTS

- Seed bank based-revegetation can support passive river management.
- We compare seed bank composition between seven river reaches of varying condition.
- Seed banks reflect changes in vegetation associated with riparian degradation.
- Terrestrial and exotic seeds dominate the seed banks of degraded river reaches.
- Seed bank-based revegetation may be best applied to highly degraded river reaches.

GRAPHICAL ABSTRACT



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ABSTRACT

Anthropogenic disturbance has contributed to widespread geomorphic adjustment and the degradation of many rivers. This research compares for river reaches of varying condition, the potential for seed banks to support geomorphic river recovery through vegetation regeneration. Seven river reaches in the lower Hunter catchment of south-eastern Australia were assessed as being in poor, moderate, or good condition, based on geomorphic and ecological indicators. Seed bank composition within the channel and floodplain (determined in a seedling emergence study) was compared to standing vegetation. Seed bank potential for supporting geomorphic recovery was assessed by measuring native species richness, and the abundance of different plant growth forms, with consideration of the roles played by different growth forms in geomorphic adjustment. The exotic seed bank was considered a limiting factor for achieving ecological restoration goals, and similarly analysed. Seed bank native species richness was comparable between the reaches, and regardless of condition, early successional and pioneer herbs, sedges, grasses and rushes dominated the seed bank. The capacity for these growth forms to colonise and stabilise non-cohesive sediments and initiate biogeomorphic succession, indicates high potential for the seed banks of even highly degraded reaches to contribute to geomorphic river recovery. However, exotic propagules increasingly dominated the seed banks of moderate and poor condition reaches and reflected increasing encroachment by terrestrial exotic vegetation associated with riparian degradation. As the degree of riparian degradation increases, the resources required to control the regeneration of exotic species will similarly increase, if seed bank-based regeneration is to contribute to both geomorphic and ecological restoration goals.

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1. Introduction

Anthropogenic disturbances such as river regulation and the clearing of riparian vegetation have contributed to widespread geomorphic adjustment and the degradation of rivers across the globe (Galay, 1983; Nilsson and Berggren, 2000). In the last three decades, river management has been globally transformed into a multi-disciplinary enterprise that addresses a great diversity of river values and ecosystem needs (Fryirs et al., 2008; Piegay et al., 2008; Rowntree and Du Preez, 2008; Wohl et al., 2008; Fryirs et al., 2013). Part of this transition is the recognition that once deterioration in riparian condition begins, it is not only costly and difficult to arrest, but even mild deterioration can significantly impair freshwater ecosystems (Hobbs and Harris, 2001; Chessman et al., 2006). Part of a modern approach to river rehabilitation and repair is to work with rivers that are in good or moderate condition to enhance recovery (Rutherfurd et al., 2000; Brierley and Fryirs, 2005, 2008; Ayres et al., 2014). As part of this approach, passive restoration techniques associated with vegetation management are becoming more popular (De Steven et al., 2006; Vosse et al., 2008; Hough-Snee et al., 2013). One aspect of passive restoration that is receiving more recent attention is how to better utilise riparian seed banks in order to support the rehabilitation of vegetation and riparian condition (Middleton, 2003; Nishihiro et al., 2006; Boudell and Stromberg, 2008; Jensen et al., 2008; Vosse et al., 2008; O'Donnell et al., 2015).

Seed banks are recognised as a potential seed source for revegetation associated with ecosystem restoration (ter Heerdt and Drost, 1994; Brock and Rogers, 1998; Middleton, 2003; Bossuyt and Honnay, 2008; Boudell and Stromberg, 2008; Vosse et al., 2008; Marchante et al., 2011; Cui et al., 2013). There has been hope that in degraded environments the seed bank may harbour native species that are able to establish given appropriate active above-ground management strategies. The removal of exotic species, the application of germination promoters such as smoke and related extracts, disturbance of topsoil, removal of livestock grazing and the alteration of inundation or watering regimes are but a few examples of such management approaches (Roche et al., 1997; Crosslé and Brock, 2002; Sarr, 2002; Thomas et al., 2003; Vosse et al., 2008; Marchante et al., 2011; Ruwanza et al., 2013; Sarneel et al., 2014).

In riparian zones, consideration of seed bank-based revegetation has rarely extended beyond the regeneration of floodplain vegetation (Brock and Rogers, 1998; Middleton, 2003; Robertson and James, 2007; Boudell and Stromberg, 2008; Williams et al., 2008; Greet et al., 2012). However, for unstable river reaches prone to erosion, bank slumping and channel widening, it is recognised that re-establishing both channel and floodplain vegetation can aid geomorphic recovery through stabilising sediment, introducing roughness to the channel and promoting deposition (Hupp, 1992; Abernethy and Rutherfurd, 1998; Corenblit et al., 2009b). Whilst these functions might be equally performed by native or exotic species, the regeneration of primarily native riparian plants would support other restoration goals associated with the enhancement of native biodiversity, including aesthetic improvements and the provision of habitat for native fauna. However, to what extent does riparian degradation change the capacity of the seed bank to support geomorphic recovery and contribute to native plant diversity?

Close to two decades of research has revealed some common strengths and limitations of seed banks for riparian revegetation, with different implications for their support of geomorphic *versus* general ecological river recovery. Riparian seed banks are often species rich, owing to seed inputs from both upstream and local vegetation assemblages, and frequently contain many species in addition to those immediately observed in the standing vegetation (Jansson et al., 2005; Capon and Brock, 2006; Webb et al., 2006; Williams et al., 2008; O'Donnell et al., 2015). However, ruderal or pioneer species and early successional growth forms typically dominate the seed bank, limiting the regenerative potential for shrubs and trees (Middleton, 2003; Capon and Brock, 2006; Hopfensperger, 2007; Bossuyt and Honnay, 2008; Williams et al., 2008). From a biogeomorphic standpoint, trees (and the wood they provide) possibly exert the greatest influence on riparian geomorphology, however early successional growth forms such as herbs, grasses, sedges and rushes also perform important functions such as stabilising sediment and introducing roughness to river channels (Hupp and Simon, 1991; Hupp, 1992; Abernethy and Rutherfurd, 1999; Erskine et al., 2009). Fast growing annual herbs, sedges and rushes are often the first to colonise and improve the stability of frequently inundated and disturbed sediments such as bars, and initiate channel contraction processes *via* bench growth (Hupp, 1992; Pywell et al., 2003; Corenblit et al., 2009b). Early successional species also modify conditions such as moisture and nutrient retention in bare sediment or soils that can facilitate the establishment of later-successional species, whether they recruit naturally or are purposefully planted, thus potentially supporting both geomorphic and ecological recovery (Prach et al., 2001).

Perhaps the greatest challenge associated with seed bank-based revegetation is the presence of exotic and invasive species in the seed bank (Williams et al., 2008; Tererai et al., 2014). Indeed the ability to form a seed bank is one of a number of traits that have contributed toward the success of many invasive species (Pyšek and Richardson, 2007). In terms of geomorphic river recovery, exotic species may perform useful functions. Historically exotic species have often been planted with the aim of fulfilling particular geomorphic goals, such as the planting of willows (*Salix* spp.) to aid bank stabilisation (Brooks and Lake, 2007). In many cases however, the intentional or unintentional presence of exotic species along rivers has contributed to adverse ecological or environmental effects, not to mention other unexpected geomorphic issues. Dense willow assemblages for example, were found to force the diversion of water and cause bank erosion in other locations (Brooks and Lake, 2007). In many cases, issues stem from exotics being ill-adapted to local conditions, such as the inadequacy of introduced *Acacia* species' root development to withstand discharges associated with some South African flood regimes, or willows exacerbating drought conditions in arid Australia through their high rates of water extraction (D'Antonio and Meyerson, 2002; Brooks and Lake, 2007). In more recent times, the active removal or control of exotic species has become a key component of river management and restoration activities in many countries (*e.g.* Holmes et al., 2005; Shafroth et al., 2005; Brooks and Lake, 2007). As such, seed bank-based regeneration to support geomorphic river recovery should aim to be consistent with these other ecological or environmental restoration goals.

Within riparian systems, the establishment and succession of vegetation and the formation of seed banks are governed by dynamic processes that are easily affected by riparian degradation. The clearing of native vegetation for example, will reduce native propagule inputs to seed banks. Equally, the encroachment of exotic species associated with anthropogenic disturbance increases exotic propagule input, with the river providing an effective conduit for the hydrochoric (water-mediated) dispersal and the deposition of propagules within seed banks (DeFerrari and Naiman, 1994; Richardson et al., 2007; Nilsson et al., 2010). Flowing water and associated fluvial processes – the erosion, transport and deposition of sediment – may equally remove or disturb existing plant assemblages, deposit propagules on sediment surfaces, or facilitate the formation of seed banks in deposited sediments (Goodson et al., 2001, 2003; Gurnell et al., 2008). The influence of these processes varies laterally and with increasing elevation from the channel bed to the floodplain, increasing the spatial complexity of disturbances (Amoros and Bornette, 2002; Lite et al., 2005; O'Donnell et al., 2014). In contrast, simplification of geomorphic structure is likely to reduce the spatial complexity of seed bank deposition, with flow on effects for the diversity of plant assemblages regenerating from the seed bank (Bendix and Hupp, 2000).

Our primary objective was to investigate the potential for seed banks to support the geomorphic recovery of degraded rivers through the regeneration of vegetation. We focus on seven river reaches ranging in condition from poor through to moderate and good in the Wollombi subcatchment of south eastern Australia. We assess seed bank potential by measuring native species richness, and the abundance of different plant growth forms, with consideration of the various roles played by different growth forms in geomorphic adjustment. Secondly, we examine species richness and growth form composition of the exotic component of the seed bank, which we consider (in most cases) a limiting factor in riparian revegetation for environmental and ecological river restoration goals. Our aim was to assess the impact of riparian deterioration on the potential for riparian seed banks to support geomorphic and ecological river recovery.

2. Materials and methods

2.1. Regional setting

This study was carried out in the Wollombi Brook subcatchment, located in the south of the Hunter River catchment of New South Wales, Australia (Fig. 1). The subcatchment drains an approximate area of 340 km^2 at the township of Wollombi, and elevation ranges from a maximum of 550 m to 85 m. Triassic sandstone and some shales dominate the geology of the region, resulting in sand-dominated rivers throughout the catchment, with gravels present in some upper reaches. Annual rainfall is approximately 900 mm and the local flood regime is considered flashy by world standards (Erskine, 1996; Erskine and Melville, 2008).

European settlement in the region began in 1823 and vegetation on the floodplains and along river channels was largely cleared for the development of agriculture. Whilst hillslopes were initially cleared, they were subsequently abandoned, allowing much regeneration of vegetation in the last 50 years. Since the peak of settlement around 1856, the population and extent of agriculture has declined (Bloomfield, 1954; Robinson, 1959; Grady, 1963; Parkes, 1979). The de-intensification of land use in the last two decades has resulted in the significant return of vegetation adjacent to and within the channel of Wollombi Brook (Erskine and Chalmers, 2009). Considerable changes in the dominant vegetation assemblages have occurred since European settlement. Palynological records indicate that prior to European settlement, channel margins contained wet sclerophyllous plant assemblages characterised by trees such as *Tristaniopsis laurina* (water gum) and *Acmena smithii* (lilly pilly) and understorey ferns, while open forest associations containing *Eucalyptus*, *Angophora* and *Melaleuca* species characterised the floodplains (Bennett and Mooney, 2003). Current assemblages contain a greater dominance of *Acacia* species in the overstorey, with exotic species and significantly more grasses and sedges dominating the understorey (Bennett and Mooney, 2003). *Casuarina cunninghamiana* is currently the dominant riparian tree species in these settings.

Extensive research by Erskine and Melville (2008), Erskine (1994, 2008), Melville and Erskine (1986) and Fryirs et al. (2012) has thoroughly documented the evolutionary development of upper Wollombi Brook since the early-mid-Holocene and, in particular, since European settlement. To summarise, the largest flood since European settlement in 1823 had a discharge of around 380,000 ML/d (4400 m^3 s^{-1}) at Payne's Crossing (Erskine and Peacock, 2002) (Fig. 1), approximately 15 km downstream of Wollombi township (catchment area of 1064 km^2). A series of small but destructive floods occurred in 1927 and 1929. The 1927 flood (discharge of 170,000 ML/d at Warkworth, 50 km downstream of Wollombi; catchment area of 1848 km^2)

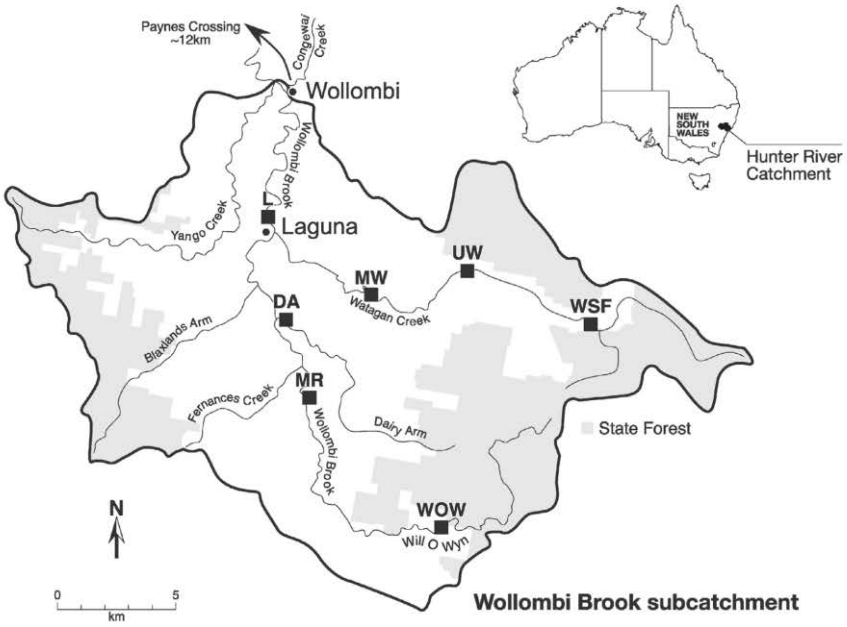

Fig. 1. Map of the Wollombi subcatchment of the Hunter River catchment, New South Wales Australia, indicating the location of the seven study reaches. Will O Wyn (WOW), Murrays Run (MR) and Laguna (L) situated along Wollombi Brook; Watagan State Forest (WSF), Upper Watagan (UW) and Mid Watagan (MW) situated along Watagan Creek; and a reach at Dairy Arm (DA).
Map modified from Erskine and Melville (2008) and O'Donnell et al. (2014).

triggered the start of what developed into significant river erosion associated with channel incision, headcut retreat and channel expansion. A resulting sediment slug in the mid-catchment now holds around 1.2 million tonnes of sand (Erskine, 2008). A series of large flood events occurred through the 1940s, of which the 1949 flood caused the most destruction. Around 2.5 km of further incision and headcut retreat occurred, transforming the middle reaches of Wollombi Brook from a sinuous, small capacity, well vegetated channel with pools to a straighter, sandier, vegetation-free, incised channel (Erskine and Melville, 2008). These headcuts have not yet extended into the most upstream reaches (around Will-O-Wyn) and the sediment slug has not yet reached the most downstream reaches (near Laguna). The second largest flood on record occurred in 2007 with a discharge of 120,000 ML/d (1392 $m^3 s^{-1}$). This flood was relatively geomorphically ineffective in comparison to previously recorded floods, which has been attributed to the vegetation that had become established within the channel since the 1950s (Fryirs et al., 2012).

2.2. Study reaches

We selected seven reaches for study that are located on three streams in the catchment (Fig. 1). The three study reaches along the Wollombi Brook trunk stream were located in the upper reaches around Will-O-Wyn (study reach WOW), mid reaches around the section known as Murrays Run (MR), and lower reaches around the township of Laguna (L). The three study reaches situated along Watagan Creek, a major tributary of Wollombi Brook, were located upstream within the Watagan State Forest (WSF), and along upper middle (UW) and middle reaches (MW). A seventh study reach was located at Dairy Arm (DA), a smaller tributary of Wollombi Brook toward the middle of the catchment (Fig. 1).

2.3. Geomorphic and riparian condition assessment of the study reaches

We employed two methods to assess the condition of each of the seven study reaches. Firstly, we conducted a geomorphic condition assessment using procedures detailed in Stage 2 of the River Styles framework (Brierley and Fryirs, 2005). Eleven geoindicators and associated desirability criteria were used to assess the geomorphic condition of a range of channel attributes, river planform and bed character at each study site (Supplementary information Table S1). The criteria were developed based on procedures established for assessing the geomorphic condition of the three sand-bed River Styles found in this system: 1) Partly confined valley with meandering planform-controlled discontinuous floodplain (reach MW), 2) partly confined valley with low-sinuosity planform-controlled discontinuous floodplain (reaches UW, L, MR and DA), and 3) confined valley with occasional floodplain pockets (reaches WOW and WSF) (Brierley and Fryirs, 2005). Geomorphic condition is assessed by determining whether the reach under investigation has the character and behaviour expected for a reach of that River Style (Brierley and Fryirs, 2005). Depending on the number of criteria met, the reach is assigned a rating of good, moderate or poor condition (Supplementary information Table S2a).

Our second assessment system was the Rapid Appraisal of Riparian Condition (RARC) (Jansen et al., 2005) developed for the Australian Government (then) Department of Land and Water (download available from www.amyjansen.com/rarc/). The framework is largely vegetation-based, and assesses factors such as proximity of the reach to intact patches of vegetation (local habitat), canopy cover and width of the riparian strip, the density of ground cover, understorey and canopy vegetation, estimates of native and exotic plant species density, and finally, the presence of key habitat features such as woody debris, hollow bearing trees, tussock grasses and reeds. Each river reach was assessed according to the standard RARC protocol. Indicators were assessed along four transects of each of the seven study reaches, arranged approximately 25–50 m apart and perpendicular to the channel. An index out of 50 is converted to a condition rating of very poor (<25), poor (25–30), average (30–35), good (35–40) and excellent (>40).

We converted the results of the River Styles geomorphic condition assessment to a score out of 50 and combined these with the results of the RARC assessment (index/50) to generate an overall riparian condition index (index/100) incorporating geomorphic and ecological attributes.

2.4. Sediment sampling and seed bank analysis

Samples of sediment were collected in November 2011 in order to determine seed bank composition. Sediment cores 5 cm in diameter and 10 cm depth were extracted from three geomorphic landforms at each of the seven sites: (1) within-channel depositional landforms (either bars or benches depending on which was available), (2) the channel bank and (3) the floodplain. Sampling both within the channel and the floodplain ensures capture of seeds dispersed *via* hydrochory as well as by animals, wind and direct seed fall (O'Donnell et al., 2015). At each site, locations for each of the three geomorphic landforms were identified for sampling. At each sampling location, three sediment cores were extracted from random positions within a 2 m^2 quadrat and then pooled into a 600 cm^2 sample. This resulted in three replicate 600 cm^2 samples for each bar/bench, bank and floodplain location, at each of the sites. All samples were stored in plastic ziplock bags and refrigerated at 4 °C until commencement of the seedling emergence experiment approximately 2 weeks later.

To determine the composition of the germinable seed bank (those species which germinate readily, without requiring specific treatment to break dormancy), we conducted a seedling emergence experiment in the Macquarie University glasshouse facility. Each pooled sediment sample was spread evenly over a 3–4 cm deep base of 50:50 native potting mix (Osmocote® Professional — Native Potting and Planting Mix) and washed river sand in a seedling tray measuring 28 × 32 cm. The seedling trays containing samples were randomly located within a single glasshouse and randomly relocated every fortnight. The samples were exposed to ambient day and night cycles and temperatures between 18 and 25 °C. Samples were mist-watered as many times daily as required to keep the samples moist but not waterlogged. After two months in the glasshouse, a small amount of fertiliser (Osmocote® Plus Trace Elements — Native Plants [NPK ratio 17.9:0.8:7.3]) was added to each seedling tray to reduce the effect of nutrient loss due to leaching and the growth of seedlings. All emergent seedlings were identified to species level where possible, or otherwise to genus level, tallied and removed from the seedling trays. Seedlings unable to be identified were re-potted in potting mix and allowed to grow until flowering. A number of fern species emerged from spores present in the seed bank, and several seedlings clearly regenerated from stem or root fragments. As these species were included in our final species tally, our study focuses on the greater 'propagule bank', which includes seeds, spores, buds and vegetative fragments, however for simplicity we refer to this as the 'seed bank'.

2.5. Vegetation survey

In October 2011, a vegetation survey of within-channel geomorphic units, bars and benches, as well as the channel banks and floodplain were conducted at each of the seven study reaches. Within each study reach, where possible, six 1 m × 1 m quadrats were used to sample representative bars and benches, and randomly selected bank and floodplain locations along a 100 m length of river. Not all study reaches contained enough bar or bench surface to accommodate 6 independent quadrats. As a result, only one and two bar quadrats were surveyed at reaches WOW and MR respectively, and five bench quadrats were surveyed at reach L. Five floodplain quadrats and five bank quadrats were surveyed at the DA and UW reaches, respectively. All plants within each quadrat were identified to species level where possible and the

percentage cover of each estimated visually. Some immature herbs and a number of uncommon grasses, sedges and rushes that were not in flower at the time of the survey were not identified. Larger shrub and tree species not captured within the quadrats were also identified. A second vegetation survey was conducted in April 2013, with the aim of capturing additional species to those observed in the October 2011 survey. New species observed in the second vegetation survey were incorporated into the list of species observed in the first survey. All plant species names conform to the Flora of New South Wales Volumes 1–4 (Harden, 1990, 1991, 1992, 1993).

Each species identified in the vegetation survey and seedling emergence experiment was assigned a growth form according to PlantNET (Botanic Gardens Trust, 2012), an online database for the flora of New South Wales (based on Harden, 1990, 1991, 1992, 1993).

2.6. Data analysis

2.6.1. Native plant species richness and the proportion of exotic species

We aimed to compare both native plant species richness and the proportion of exotic plant species richness in the both seed bank and standing vegetation between the seven reaches representing good, moderate and poor condition. It was not feasible to statistically compare poor, moderate and good condition classes in a General Linear Mixed Model (GLMM), as there was insufficient replication for the Condition class. As such, native plant species richness was compared between reaches using General Linear Models with a normal distribution and identity link function. Generalised Linear Models with a binomial distribution and logit link function were employed to analyse the proportion of exotic species, as this approach accounted for differences in total species richness between the units and reaches. This approach is used for binary data, in this case 'exotic' or not (native). For each sample, the response variable is derived from the number of exotic species detected (referred to as 'successes') and the total number of species detected (referred to as 'trials') (Cox and Snell, 1981). Measures of species richness were square root transformed to achieve normality. All models contained the fixed factors Reach (seven levels) and Unit (3 levels: bar/bench, bank and floodplain). For both analyses, reduced models were compared to the full model using Likelihood Ratio (LR) tests. When Reach was found to be a significant factor we performed post-hoc Tukey tests to compare the good, moderate and poor riparian condition reaches. GLMs and post-hoc comparisons were performed in R (v. 2.15.1) (R Development Core Team, 2008), using the lme4 (Bates et al., 2013) and multcomp (Hothorn et al., 2008) packages, respectively.

2.6.2. Proportions of native and exotic plant growth forms

We compared the seven reaches in terms of the different proportions of native and exotic plant species growth forms found in the seed bank. This was then repeated for the standing vegetation to detect any significant differences in the general plant assemblages that characterise the reaches of different condition. Secondly, we compared the proportion of different plant growth forms between the seed bank and vegetation for native and exotic species to investigate the relationship between the seed bank and standing vegetation across reaches of different condition. This analysis was conducted for each reach separately. Finally, to investigate the dominance of the seed bank by certain growth forms and whether this changes with condition, we compared the abundance of seed bank propagules belonging to each growth form type between the seven reaches.

To compare the proportions of different plant growth forms (tree, shrub, shrub/tree [species that can take either form depending on environmental conditions], fern, grass, herb, sedge/rush and vine), for the species found in the standing vegetation survey and/or detected in the seed bank, we used Chi square tests for association using SPSS v.20 (SPSS Inc., 2011). Fisher's exact tests (FET) were most commonly calculated due to the small sample sizes. The significance of the proportional differences between each growth form for each reach was estimated using Bonferroni rcalculations. The data were separated into native and exotic species. Counts for each growth form were too low to allow separate analysis of each geomorphic location (bar/bench, bank and floodplain). As such, we analysed each reach as a whole, by summing growth form counts for all geomorphic location replicates. The abundance of propagules belonging to each growth form type was also compared between sites using Chi square analyses. Counts for native and exotic species were analysed between the reaches separately.

3. Results

3.1. Results of condition analyses

The results of the River Styles geomorphic condition assessment (Supplementary information Table S2b) and the Rapid Appraisal of Riparian Condition (RARC) (Supplementary information Table S3) produced similar results across the seven reaches. DA was consistently rated as poor and WOW and WSF as good. Three reaches (L, MR and MW) received similar scores to each other in both assessment systems and UW was identified as being in better condition than these reaches but poorer in condition than WOW and WSF. The RARC ratings of condition were generally lower than the River Styles condition assessment. Our final determination of condition, based on the combined scores of both assessment systems were: DA: poor; L, MR and MW: lower moderate, UW: upper moderate and WOW and WSF: good (Supplementary information Table S4).

3.2. Seed bank composition relative to standing vegetation

A total of 228 plant species representing 23 plant families were identified in the seedling emergence trial and vegetation survey. Of these, 34 species were restricted to the seed bank, 124 species restricted to the standing vegetation and 67 species detected in both. In the seedling emergence study, 3336 seeds representing 100 species were detected. Total species richness (seed bank and standing vegetation) across the seven study reaches ranged from 66 (61% exotic species) at the poor condition site (DA) to 95 (32% exotic species) at one of the good condition sites, but showed some variability across the moderate condition and the second of the good condition sites (Table 1). The number of species present in the standing vegetation that were also represented in the seed bank showed no clear trend with reach condition. The number of native and exotic species detected solely in the seed bank similarly showed no clear trend with reach condition (Table 1).

3.3. Native plant species richness

The native plant species richness of the seed bank was highly variable, such that no significant differences were found between the seven study reaches. Similarly there were no significant differences between bars/benches, bank and the floodplain (Fig. 2a). In comparison, native species richness of the standing vegetation was much less variable. The relative native species richness of bar/bench, bank and floodplain vegetation varied depending on the reach in question (GLM, Reach * Unit interaction, $\chi^2_2 = 3.0654$, $p = 0.006$). Poor and moderate condition sites had comparable native species richness across bars/benches, banks and the floodplain. For the two good condition reaches however, the native species richness of the floodplain was significantly higher than bars/benches, as was the native species richness of the banks at the WOW reach (GLM, WSF: $F_{2,21} = 7.616$, $p < 0.003$; WOW: $F_{2,16} = 13.813$, $p < 0.001$).

3.4. The proportion of exotic species

The proportion of exotic species in the seed bank differed significantly between sites ($\chi^2_6 = 72.685$, $p < 0.001$), with the two good

Table 1
Summary of reach-scale total native and exotic species richness compared between the seed bank and standing vegetation.

Site	Condition	Total species richness	Proportion of exotic species	No. (and %) of standing vegetation species detected in seed bank		No. (and %) of species within the reach detected only in the seed bank	
				Native	Exotic	Native	Exotic
DA	Poor	66	0.61	9 (39)	23 (44)	3 (12)	8 (20)
MR	Lower moderate	76	0.57	7 (30)	23 (52)	10 (30)	12 (28)
L	Lower moderate	82	0.51	7 (23)	21 (48)	10 (25)	13 (31)
MW	Lower moderate	88	0.42	11 (37)	18 (44)	21 (41)	21 (57)
UW	Upper moderate	76	0.38	11 (31)	18 (54)	12 (26)	16 (55)
WSF	Good	87	0.22	4 (8)	5 (9)	16 (24)	8 (42)
WOW	Good	95	0.32	12 (26)	14 (10)	18 (28)	10 (33)

condition reaches (WSF, WOW) having significantly lower proportions of exotic species in the seed bank than the poor condition reach and all four moderate condition reaches (Tukey site comparisons – WOW/DA: $z = -4.031$, $p = 0.001$; WSF/DA: $z = -4.989$, $p < 0.001$; WOW/L: $z = -4.608$, $p < 0.001$; WSF/L: $z = -5.737$, $p = 0.001$; WOW/MR: $z = -4.569$, $p < 0.001$; WSF/MR: $z = -5.691$, $p < 0.001$; WOW/MW: $z = -3.841$, $p = 0.002$; WSF/MW: $z = -4.844$, $p < 0.001$; WOW/UW: $z = -3.643$, $p = 0.005$; WSF/UW: $z = -4.597$, $p < 0.001$) (Fig. 2b). There were no significant differences between the moderate and poor condition reaches or between the two good condition reaches. The proportion of exotic species in the seed bank did not significantly differ between the bars/benches, banks or the floodplain for any of the reaches. In contrast, for the standing vegetation, we found that the relative proportions of exotic species in bars/benches, banks and the floodplain differed significantly across the sites (GLM, reach*unit interaction, $\chi^2_2 = 18.268$, $p < 0.001$). For the two good condition sites and two of the moderate condition reaches (MW and UW), the proportion of exotic species was consistent across the three geomorphic locations (Fig. 2b). However, the standing vegetation of the floodplain had significantly greater proportions of exotic species than both the bars/benches and banks at the poor condition reach (GLM, $\chi^2_2 = 10.797$, $p = 0.005$) and greater proportions than the bars/benches at the two lower moderate condition reaches (L and MR) (GLM, L: $\chi^2_2 = 10.43$, $p = 0.005$; MR:$\chi^2_2 = 6.6794$, $p = 0.035$).

3.5. Growth form proportions of native and exotic species and propagules

When the species in the seed bank were examined, we found no significant difference between any reaches with respect to the proportion of species belonging to each growth form (tree, shrub, fern, grass, herb, sedge/rush and vine). This was true for both native and exotic species in the seed bank. We also found this to be the case for the standing vegetation. Across the seven reaches however, there were differences in the comparative species richness of different plant growth forms between the seed bank and standing vegetation (Table 2). For the native species, there was no obvious trend related to reach condition. The seed bank of the majority of reaches, regardless of condition, had more sedge and rush species and fewer shrub species than that found

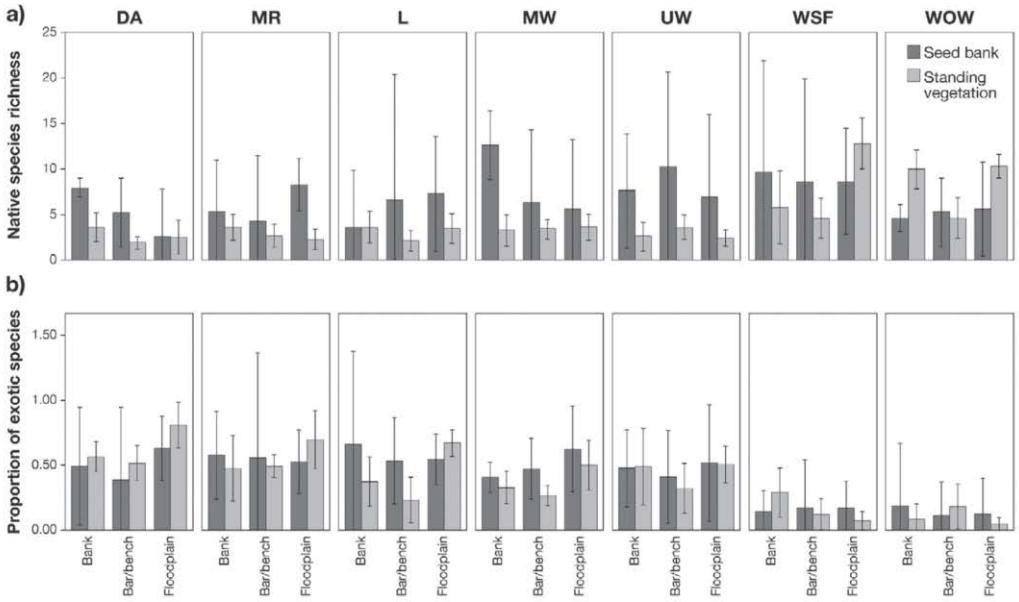

Fig. 2. Native and exotic species richness of the seed bank and standing vegetation compared between the seven study reaches. Mean a) native species richness and b) proportion of exotic plant species, detected in the seed bank and standing vegetation of three geomorphic locations: bank, bar/bench and floodplain, of seven river reaches of varying geomorphic condition (DA: poor; MR, L, MW: lower moderate; UW: upper moderate; WSF, WOW: good) within the Wollombi subcatchment. Error bars represent 95% confidence intervals.

in the standing vegetation. Only the poor site had a greater number of grass species in the seed bank, while one good site (WSF) had fewer grass species in the seed bank than observed in the standing vegetation (Table 2). For the exotic species, the proportions of different growth forms between the seed bank and standing vegetation were comparable for the poor reach and the two lower moderate condition reaches (L and MR). For the two lower and upper moderate condition reaches (MW and UW, respectively) and two good reaches however, there were weak but significant differences in growth form proportions. Of note, greater numbers of exotic sedge and rush species were present in the seed bank in comparison to the standing vegetation at three of the sites (UW, WOW, WSF) (Table 2). Vine species were not detected in the seed bank at any site.

The total number of native and exotic propagules detected in the seed bank showed no consistent trend in relation to riparian condition (Fig. 3a). However, the three lowest-scoring reaches (DA, L, MR) had the highest proportion of exotic propagules, comprising greater than 50% of their seed bank (Fig. 3a). The native seed bank of the good condition and upper moderate condition reaches were generally more diverse, yet sedges and rushes dominated at all reaches (Fig. 3b). The two good condition reaches contained significantly greater proportions of shrub/tree seeds than all other reaches ($\chi^2_{30,\,N\,=\,1702} = 222.271$, $p < 0.001$). Proportions of native tree, shrub, grass and sedge/rush propagules were mostly comparable across all sites, but ferns were not present in the poor condition reach (DA), lower moderate condition reaches (DA, L, MR) or the upper moderate condition reach (UW). The exotic seed bank was less diverse than the native seed bank and lacked any species in the tree and shrub/tree categories (Fig. 3c). The proportional abundance of propagules for all remaining growth forms differed significantly between the reaches, with the exception of shrubs, which were only present at the poor and two lower moderate condition reaches (DA, L and MW) ($\chi^2_{30,\,N\,=\,1633} = 446.383$, $p < 0.001$). Exotic herbs dominated the seed bank of the poor and two lower moderate (MR, L) condition reaches, whereas sedges and rushes dominated the good condition reaches. The abundance of grass propagules was highly variable across the reaches.

4. Discussion

This study aimed to assess the potential of the seed bank to contribute to vegetation regeneration to support geomorphic recovery, across seven reaches of varying condition. Our results revealed significant scope for the seed banks of poor and moderate condition river reaches to contribute to the regeneration of non-woody vegetation (*e.g.* herbs, grasses, sedges and rushes). The seed banks of these reaches were generally abundant, and displayed a similar range of growth forms and comparable native species richness to the seed bank of good condition sites. However, the seed banks of poor and lower moderate condition reaches were also clearly distinguished by a high proportion of exotic propagules, and increasingly dominated by terrestrial herbs and grasses with declining condition. The native component of the seed bank was also less diverse than that of good and upper moderate condition reaches, and contained significantly fewer shrub/tree seeds than good condition reaches. Based on these results, we suggest that the utility of the seed bank to support geomorphic river recovery through the regeneration of vegetation will depend on the nature of the geomorphic change desired, and the wider aims of river restoration projects.

4.1. Riparian condition, seed bank-based vegetation regeneration and the support of geomorphic recovery

The seed banks of reaches in poor and moderate condition all had a number of characteristics that hold promise for use in the regeneration of riparian vegetation. Firstly, the abundance of propagules at these sites were comparable, if not greater, than that detected at the good condition sites, suggesting adequate potential for regeneration. Secondly, the seed banks of poor and moderate condition reaches were species rich, often containing twice the number of native species observed in the standing vegetation, and in some cases were as rich as the standing vegetation observed at good condition reaches (Fig. 2a). Seed bank native species richness was also comparable across bars, benches, the river bank and floodplain across all reaches (Fig. 2a). Considering the influence of environmental conditions on the assemblage of species regenerating from the seed bank (*e.g.* Levine and Stromberg, 2001; Robertson and James, 2007; Reid and Capon, 2011), high propagule abundance and species richness effectively broaden the range of environmental conditions that may result in plant regeneration. We observed comparable seed bank species richness between the seven reaches, which was consistently higher than that observed in the standing vegetation at all but the good condition reaches.

Riparian condition did not affect the tendency for the seed bank to be dominated by ruderal and early successional plant growth forms

Table 2
Chi square analysis results. Fisher's exact test (FET) testing associations between the seven river reaches and the proportion of 8 different plant growth forms for a) native species and b) exotic species. The riparian condition of each is in parentheses following reach name: (P) poor, (M) moderate and (G) good. "+": proportion of growth form higher in the seed bank than standing vegetation, "−": proportion of growth form lower in the seed bank than standing vegetation, ".": no significant difference for that growth form, "ns": no significant difference in proportions of any growth forms between seed bank and standing vegetation for the reach, "*": too few counts to compare (not included in comparisons).

Seed bank growth form proportions compared to standing vegetation									
Reach	FET significance	Growth form							
		Fern	Grass	Herb	Shrub	Sedge/rush	Shrub/tree	Tree	Vine
Native species									
DA (P)	$p < 0.001$	.	+	.	−	+	.	.	−
L (LM)	$p < 0.001$	−	.	+	−	+	.	.	−
MR (LM)	$p < 0.001$	.	.	+	−	+	.	.	−
MW (LM)	$p < 0.001$	−	.	+	−	+	.	.	−
UW (UM)	$p < 0.001$	.	.	.	−	+	.	.	−
WOW (G)	$p < 0.001$	.	.	+	−	+	.	.	−
WSF (G)	$p < 0.001$	.	−	.	.	+	.	.	−
Exotic species									
DA (P)		ns	ns	ns	ns	ns	ns	ns	ns
L (LM)		ns	ns	ns	ns	ns	ns	ns	ns
MR (LM)		ns	ns	ns	ns	ns	ns	ns	ns
MW (LM)	$p = 0.037$	*	.	.	.	.	*	*	−
UW (UM)	$p = 0.006$	*	.	.	−	+	*	*	−
WOW (G)	$p = 0.021$	*	.	.	.	+	*	.	.
WSF (G)	$p = 0.013$	*	.	.	.	+	*	*	*

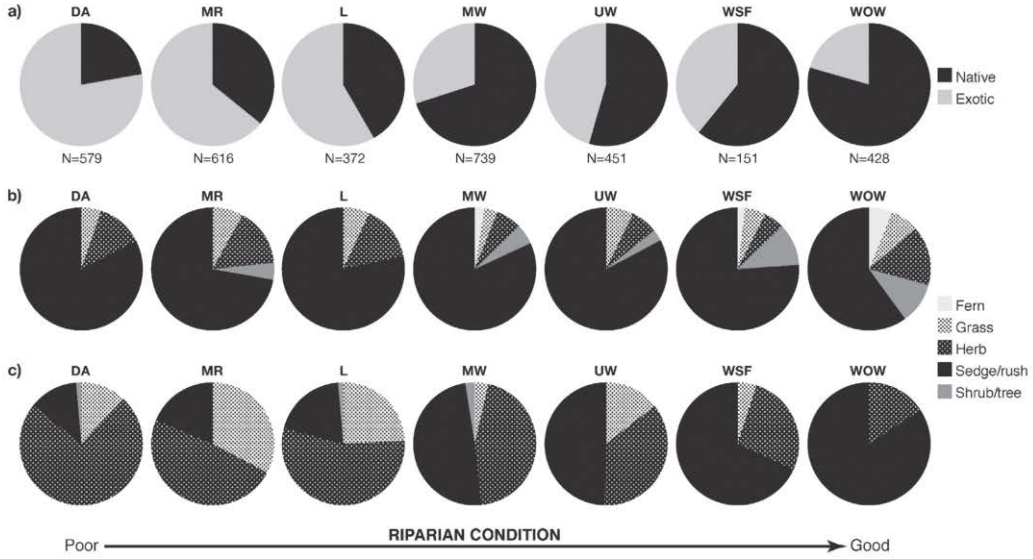

Fig. 3. Seed bank composition compared between seven reaches of varying riparian condition. Relative proportions of a) native and exotic propagules, b) native propagules of different growth forms and c) exotic propagules of different growth forms detected in the seed bank of seven river reaches of varying riparian condition (DA: poor; MR, L, MW: lower moderate; UW: upper moderate; WSF, WOW: good). Proportions for each reach are based on the combined counts of propagules detected in the seed banks of bars/benches, bank and floodplain.

including, herbs, grasses, sedges and rushes (Middleton, 2003; Capon and Brock, 2006; Hopfensperger, 2007; Bossuyt and Honnay, 2008; Williams et al., 2008). For reaches recovering from disturbance such as historical incision, channel widening or sediment slug encroachment, establishing vegetation on the channel banks and on within-channel geomorphic units such as bars and benches is the first crucial step for stabilising sediments, increasing channel roughness and encouraging deposition (Hupp and Rinaldi, 2007; Corenblit et al., 2009a). We found the seed bank should be highly capable of fulfilling this role. Fast growing annual herbs for example, are often the first and only plants able to establish on these frequently inundated and non-cohesive geomorphic units (Hupp, 1992). Grasses are also very effective at mechanically stabilising bank sediments through their root growth (Simon and Collison, 2002). Once established, these plants can stabilise sediment and initiate biogeomorphic succession and channel contraction, with reciprocal interactions between plants and geomorphology driving plant succession upon increasingly stable geomorphic units (Hupp, 1992; Corenblit et al., 2008; Corenblit et al., 2009b; Corenblit et al., 2010; O'Donnell et al., 2015). Whilst questions still remain as to the likelihood of seed banks residing in older sediments exposed by recent erosion (Goodson et al., 2002), there appears great potential for the seed banks held within the river banks and depositional geomorphic units of disturbed river reaches, to initiate vegetation regeneration.

4.2. Limitations of the seed bank for geomorphic river recovery and consideration of wider restoration goals

The underrepresentation of trees and shrubs, and to a lesser extent ferns and vines in the seed bank at all reaches regardless of condition (Table 2, Fig. 3a,b), has implications for seed bank-based regeneration aimed at both geomorphic and ecological river recovery (Leege et al., 1981, Kauffman et al., 1983, Green and Kauffman, 1995). In temperate and tropical climates, riparian vegetation is typically represented by groundcover, understory and overstorey vegetation, which together produce a level of geomorphic robustness (Howell et al., 1994; Tabacchi et al., 1998; Webb et al., 1999; Fryirs et al., 2012). Trees particularly influence hydrological and fluvial processes (*e.g.* Erskine et al., 2009). This and other research (*e.g.* Bossuyt and Honnay, 2008) has shown that utilisation of the seed bank for the establishment of trees and shrubs is limited, and other strategies such as the planting of tubestock will be required if revegetation of these growth forms is a primary aim of rehabilitation. Regardless of the recruitment source (*e.g.* seed bank, planted tube stock), in degraded reaches, the initial stabilisation of sediment by pioneer vegetation and the re-establishment of appropriate biogeomorphic processes may need to be achieved before trees will successfully establish (Scott et al., 1996; Carter Johnson, 2000; Steiger et al., 2005).

The increasingly high representation of exotic species in the seed banks of reaches with declining riparian condition also raises issues about the utility of the seed bank for restoration when wider restoration goals including biodiversity conservation are included. The active removal of exotic or invasive species is often a key goal in riparian management and restoration (*e.g.* Holmes et al., 2005; Shafroth et al., 2005; Brooks and Lake, 2007). However, exotic propagules accounted for more than 75% of the seed bank at the poor condition reach and greater than 50% in the two lower moderate condition reaches (Fig. 3a). It is now widely accepted that the eradication of all exotic species is virtually impossible in most ecosystems and a growing movement seeks to distinguish between exotic species that are fairly benign or may support restoration trajectories, from invasive or exotic species with primarily negative impacts on hydrogeomorphological processes and ecological functioning (Loope et al., 1988; Tickner et al., 2001; D'Antonio and Meyerson, 2002; Ewel and Putz, 2004; Schlaepfer et al., 2011). Geomorphic river recovery may be facilitated by plants regardless of whether they are native or exotic. However, if the reconstruction of primarily native vegetation is a goal of restoration, the level of intervention required to support native regeneration from the seed bank and control exotic species will increase with the degree of riparian degradation (Howell et al., 1994; Erskine and Webb, 2003; Holmes et al., 2005; Williams et al., 2008). Appropriate control methods will depend on the

species in question, and require consideration of the effect of the control method on the stability of sediment (Rutherfurd et al., 2000). For example, removing exotic woody vegetation along river channels may destabilise sediment and facilitate erosion (*e.g.* Rutherfurd et al., 2000; Vincent et al., 2009).

The exotic component of the seed bank tended to increase as riparian condition declined, and the seed bank increasingly reflected the terrestrialisation of vegetation that typically accompanies riparian degradation. For example, we observed a shift from sedge-, rush- and herb-dominated seed banks in good and upper moderate condition reaches, to increasingly exotic herb- and grass-dominated seed banks in lower moderate and poor condition reaches. (Fig. 3a,c). Exotic terrestrial species are often more competitive than the native riparian species when water availability is reduced due to factors such as regulation and extraction, or channel-floodplain disconnectivity associated with channel incision and widening (Jensen et al., 2008; Williams et al., 2008; Catford et al., 2011). The strong capacity for seed banks to reflect these changes in vegetation highlights the difficulty in relying solely on seed bank-based regeneration to aid geomorphic recovery and the development of native riparian vegetation assemblages. As such, degraded reaches may require action in addition to simple weed management to improve conditions for the establishment of native *riparian* species, such as the allocation of environmental flows and the planting of trees (Catford et al., 2011). Interestingly, Hough-Snee et al. (2013) observed gradual shifts from initial colonisation by annual pasture grasses and herbs such as those that dominate the exotic seed bank, to perennial herbs and riparian graminoids such as *Carex*, along streams from which cattle had been excluded. However in some cases, in the absence of management, exotic species may continue to dominate cattle-excluded river reaches even after decades (Jansen and Robertson, 2001).

On a more positive note, the seed bank may be more diverse than can be detected in simple seedling emergence trials. Some species require different germination cues to those provided under glasshouse conditions, such as temperature stratification or time for ripening. Alternative seed bank assay methods such as floatation often detect seeds in addition to those found in seedling emergence trials (Brown, 1992; Price et al., 2010). Further research into the prevalence of dormant tree seeds (and those of other growth forms) within riparian seed banks, what their germination cues are, and whether their germination could be encouraged in the field would be worthwhile (*e.g.* Merritt et al., 2007). The application of heat, smoke and related chemical extracts has successfully boosted germination from seed banks in many Australian trials, however riparian trees may be less likely to respond to fire-related cues (Roche et al., 1997; Thomas et al., 2003). For shrubs and trees that do readily emerge from the seed bank, identification and early protection in the form of shelter or barriers to reduce herbivory and trampling may increase the chance of successful establishment (Sweeney and Czapka, 2004). Currently however, re-establishing shrubs and trees within the riparian zone by direct seeding and planting in appropriate locations (*e.g.* Schneider, 2007), is likely to be much more successful than relying solely on regeneration from the seed bank.

4.3. The role of standing vegetation and seed bank inputs

The results of this study highlight the importance of intact, species rich native standing vegetation, or proximity to such vegetation, for increasing the potential of the seed bank for regeneration aimed at achieving geomorphic and ecological goals. At good condition reaches dominated by diverse native assemblages, exotic species richness in the seed bank was low, and the native component of the seed bank showed a high diversity of growth forms (Fig. 3a,b). The seed banks of poor and lower moderate condition sites, for which greater than half of the standing vegetation species were typically exotic, were dominated by exotic propagules (Fig. 2a,b) (see also Capon and Brock, 2006; Robertson and James, 2007). At the most degraded site (DA) and two moderate condition reaches (MW and UW), seed bank native species richness was greater within the channel than on the floodplain, possibly reflecting hydrochoric seed inputs from vegetation upstream (Nilsson et al., 2010). This suggests that for degraded river reaches, their position in the catchment is critical. If they are positioned downstream of, or in proximity to, reaches with relatively intact vegetation assemblages then the supply of desirable propagules along the channel, and their incorporation into the seed bank is more likely (Jansson et al., 2005; Tabacchi et al., 2005; Robertson and James, 2007). Conversely, upstream reaches, if dominated by exotic species, will supply exotic propagules to seed banks downstream (Planty-Tabacchi et al., 1996). These factors highlight the importance of maintaining diverse native vegetation along river corridors to replenish seed banks and increase their capacity to contribute to the regeneration of native riparian vegetation within catchments.

Finally, it is important to note that a range of factors in addition to the nature of local riparian vegetation will ultimately influence seed inputs to seed banks, seed bank formation, and successful regeneration from the seed bank in each specific location. For example, high rates of sedimentation may facilitate the development of deep seed banks, but also inhibit the survival of germinants (Froud-Williams et al., 1984; O'Donnell et al., 2014). Hydraulic roughness will influence the deposition and incorporation of seeds into the seed bank, and seed banks are less likely to form in non-cohesive sediments, or those prone to erosion (Goodson et al., 2002; O'Hare et al., 2012). Consideration of these and other hydrological, biogeomorphic and hydrogeomorphic factors will aid the selection of sites for which the encouragement of seed bank-based regeneration may be most successful.

5. Conclusions

The results of this study suggest that the seed banks of even heavily degraded river reaches may still contain an abundant mix of pioneer and early successional plant propagules, with the potential to contribute to the geomorphic recovery of river reaches. The clearest role for the seed bank may be in the stabilisation of the channel banks and sediment of within-channel depositional landforms such as benches and bars through the regeneration of herbs, grasses, sedges and rushes. Heavily cleared and degraded floodplains may also benefit from regeneration from the seed bank to increase the density of groundcover. The development of more diverse later-successional riparian plant communities are more likely to be achieved through a mixture of natural recruitment over time, and direct planting where natural recruitment fails to occur. Exotic species are prolific and increasingly dominate seed banks as the degree of riparian degradation increases. If regeneration from the seed bank is used in practice, decisions will need to be made as to the extent of active management, monitoring of regeneration and weed management required in each setting. In river reaches considered too degraded to consider significant investment in ongoing restoration, a more passive approach to seed bank-based regeneration, involving little or no follow-up management may provide the greatest returns for effort expended. In such reaches, the regeneration of even exotic species may support geomorphic recovery and provide some ecosystem services, such as the provision of habitat for fauna. Poor condition sites could become test cases for measuring vegetation succession and related geomorphic change trajectories following activities designed to enhance seed bank germination — in essence a test of seed-bank based rehabilitation, as opposed to restoration.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2015.10.118.

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Chapter 6

Discussion

DISCUSSION

Thesis overview

This thesis aimed to 1) examine the structure and spatial variability of riparian seed banks, 2) investigate drivers of observed seed bank characteristics, 3) assess the potential contribution of seed bank-based regeneration of riparian vegetation and geomorphic river recovery based on plant species traits, and 4) based on the findings, present implications for the use of seed bank-based revegetation to support river management and restoration goals. The approach adopted draws upon a range of different research fields including seed banks and plant ecology, geomorphology and river management. This thesis integrates research related to the study of the similarity of the seed bank to standing riparian vegetation (Middleton 2003, Robertson and James 2007, Boudell and Stromberg 2008, Williams et al. 2008, Cui et al. 2013), the role of fluvial processes (primarily sediment deposition) in seed bank formation (Goodson et al. 2003, Gurnell et al. 2008, Moggridge et al. 2009), comparative studies testing the influence of geomorphology, inundation regime and disturbance on seed bank character (Nicol et al. 2003, Webb et al. 2006, James et al. 2007, Gurnell et al. 2008) and seed bank seed traits as indicators of seed inputs (Pettit and Froend 2001, Goodson et al. 2003, Gurnell et al. 2008). The role of hydrochory (water-mediated dispersal) in influencing both riparian vegetation and seed bank diversity (Nilsson et al. 1991b, Middleton 2000, Gurnell et al. 2007a, Nilsson et al. 2010), and the influence of seed morphology on seed transport, deposition and erosion (Boedeltje et al. 2004, Vogt et al. 2006, Gurnell 2007, García-Fayos et al. 2010) were other important areas of research that contributed to this thesis.

The research presented in this thesis is firmly rooted in biogeomorphology. It contributes a novel approach to the study of riparian seed banks, by including concepts related to the reciprocal interactions between plants, geomorphology, hydrology and fluvial processes (e.g. Hupp 1992, Corenblit et al. 2007, Hupp and Rinaldi 2007). Throughout the thesis I investigate how biogeomorphic processes influence, and are influenced by, the regeneration of riparian vegetation from the seed bank. Biogeomorphic theory in combination with the study of plant species traits (c.f. Lavorel and Garnier 2002, Díaz et al. 2007), for example, were particularly important for assessing the extent to which seed bank-based regeneration may influence geomorphic river recovery.

The aims of the thesis, the research approach and relevant thesis chapters are presented in Figure 1. Chapter two (*Riparian seed bank stratification*) and chapter three (*Riparian seed banks and sedimentology*) focus on characterising the structure of seed banks within three different geomorphic units commonly found in riparian systems (bars, benches and the floodplain). This is examined in relation to the geomorphic structure and sedimentology of these units. These chapters relate patterns in seed bank species richness and abundance to the fluvial processes that influence the formation of these geomorphic units, and their resulting sedimentology. Chapter 3 discusses the direct and indirect mechanisms by which hydrology and geomorphology influence riparian seed bank inputs and losses through reciprocal interactions with vegetation. Chapters four and five focus on the traits of the species contained in the seed bank. Traits are used to assess the potential contribution of the

seed bank to riparian vegetation assemblages and their degree of influence on geomorphic structure and change. Chapter four (*Riparian seed banks and biogeomorphic succession*), compares the growth form, dispersal mechanisms and longevity of species found in the seed bank with those of the standing vegetation on bars, benches and the floodplain. This is used to assess riparian seed inputs and the potential contribution of the seed bank to each biogeomorphic (plant-geomorphic) assemblage. This study found that the seed bank supports primarily early stages of biogeomorphic succession, and thus may have a role to play in initiating important channel contraction processes in eroded and over-widened river reaches. Chapter five (*Seed banks in relation to riparian condition*) compares between seven river reaches of varying condition, the capacity of the seed bank to contribute to geomorphic river recovery through the regeneration of native plants, and assesses the prevalence of less desirable exotic species. The findings suggest that poor condition river reaches may benefit most from seed bank-based revegetation.

This final thesis discussion chapter will bring together the findings of each publication to address the thesis aims. Included is discussion of the relevance of the findings beyond the study area, and the contribution of the findings to international riparian seed bank research. To finish, I present some implications for the use of seed-bank based revegetation as a tool in river management and restoration, and highlight two important future directions for riparian seed bank research.

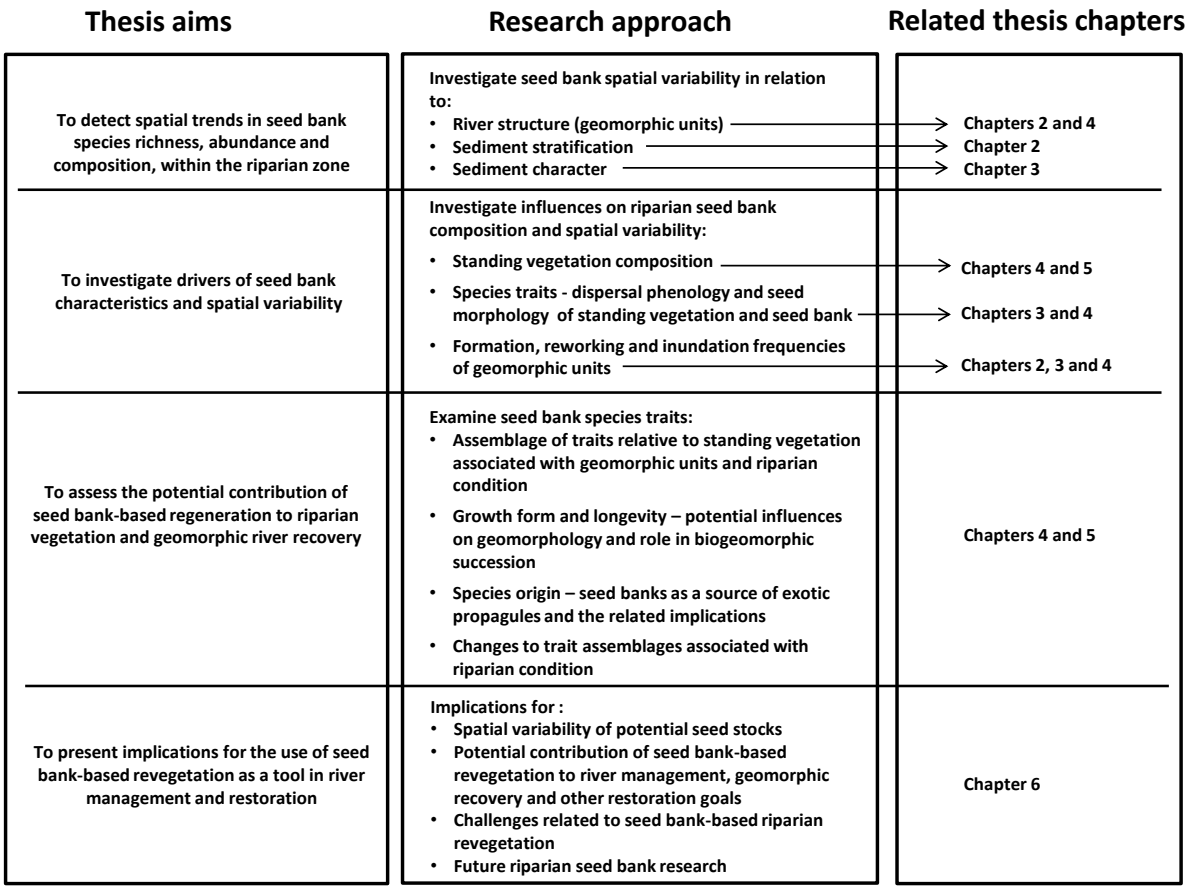


Figure 1 – Outline of thesis aims, research approach and how each chapter relates to thesis aims.

THESIS AIMS 1 & 2: Spatial trends in riparian seed bank species richness, abundance and composition and drivers of seed bank characteristics and spatial variability.

Background and research approach

Prior to 2001, little research had been conducted on the seed banks of riparian ecosystems – perhaps a testament to the complexity and dynamism of the riparian zone (Goodson et al. 2001). Since the review on riparian seed banks by Goodson et al. (2001), a significant body of seed bank research has examined the spatial complexity of

riparian seed bank characteristics and investigated how this is influenced by factors such as inundation frequency, sediment deposition and seed inputs from local vegetation (e.g. Goodson et al. 2003, Combroux and Bornette 2004, Gurnell et al. 2008, Williams et al. 2008, Moggridge et al. 2009). Many of these studies succeed in documenting fine-scale seed contributions to the seed bank, from input processes such as hydrochory and seed rain (e.g. Goodson et al. 2003, Tabacchi et al. 2005, Gurnell et al. 2008). The two first aims of this thesis (*to detect spatial trends in riparian seed bank species richness, abundance and composition and investigate drivers of seed bank characteristics and spatial variability*) draw upon this current knowledge of the factors that control seed bank inputs and formation, to better understand and ultimately predict spatial variability in seed bank qualities within river reaches.

In chapters two, three (and to some extent four), spatial trends in seed bank characteristics are examined in relation to different geomorphic units sediment qualities. Chapter two compares patterns of stratification and overall seed bank abundance and species richness within the top 30 cm of sediment in bars, benches and the floodplain. Chapter three investigates and compares the relationships between the sedimentological qualities (related to particle size and organic content) of these geomorphic units and seed bank qualities (abundance and species richness). Chapter four includes investigation of seed bank inputs, by comparing seed-dispersal mechanisms between the species assemblages characterising the seed bank and standing vegetation of bars, benches, and the floodplain. To then identify the potential *drivers* of the seed bank spatial variability observed in these different contexts, seed bank characteristics were examined in light of the factors influencing the geomorphic

form and sedimentology of bars, benches and the floodplain. These three depositional geomorphic units form at increasing elevation from the channel bed, respectively. As such, they were considered to represent a gradient of decreasing frequency of inundation and disturbance (sediment erosion/deposition/reworking). Chapters two and three explore how the form and sedimentology of each geomorphic unit is influenced by interrelated factors such as the establishment of vegetation, sediment cohesion, and the likelihood of erosion versus deposition – all of which are ultimately controlled by inundation and disturbance. For each geomorphic unit, patterns of seed bank abundance and species richness were assessed in terms of the relative influence of these different factors.

Contribution of the research findings to international seed bank research

This thesis provides three important contributions to the study of spatial variability within riparian seed banks and the drivers of this variability. Firstly, chapter two addressed a knowledge gap on riparian seed banks that was highlighted by Goodson et al. (2001). They note that whilst a few studies had investigated the depth of seed banks in lakes and marshes (Leck and Simpson 1987, Bonis and Lepart 1994, Abernethy and Willby 1999), to date no studies had comprehensively measured the vertical stratification of seed banks within a river system. This is despite the importance of this information not only for better understanding the nature of riparian seed banks and their formation, but also their capacity for vegetation regeneration after floods and other disturbance events. It was unclear whether seed banks were available at depth to facilitate vegetation regeneration after the erosion of top sediments, and how this capacity varies between geomorphic units within the channel and floodplain.

The findings of chapter two showed that bars, benches and the floodplain displayed differences in the stratification (to 30 cm) of seed bank abundance and species richness (chapter 2, Figures 3, 4). The seed banks of bars were species poor and highly variable in terms of seed abundance with depth. Bench seed banks displayed similar variability in seed bank abundance and species richness with depth to that of bars, but overall benches were significantly more species rich. In contrast, while overall seed bank species richness was comparable between the floodplain and benches, both abundance and species richness of the floodplain seed bank declined with depth. Most importantly, the findings of this study highlight the capacity for riparian ecosystems to develop deep, species-rich seed banks in zones receiving inundation at a frequency that allows the establishment of enough vegetation to stabilise sediment and promote sediment deposition. In such zones, sediment deposition aids the vertical development of the seed bank, and seed bank species richness is maximised by the input of seeds from both hydrochory during inundation events, and seed rain (from standing vegetation) between inundation events. To some extent, the findings in chapter two reflect those of Goodson et al (2002) who observed high seed bank species richness and abundance in zones of frequent deposition (in this case bank toe/bar sediments), but low seed bank abundance and species richness in older bank sediments exposed by erosion. Older sediments, such as the deeper floodplain sediments observed in chapter 2, should reflect seed loss due to seed mortality.

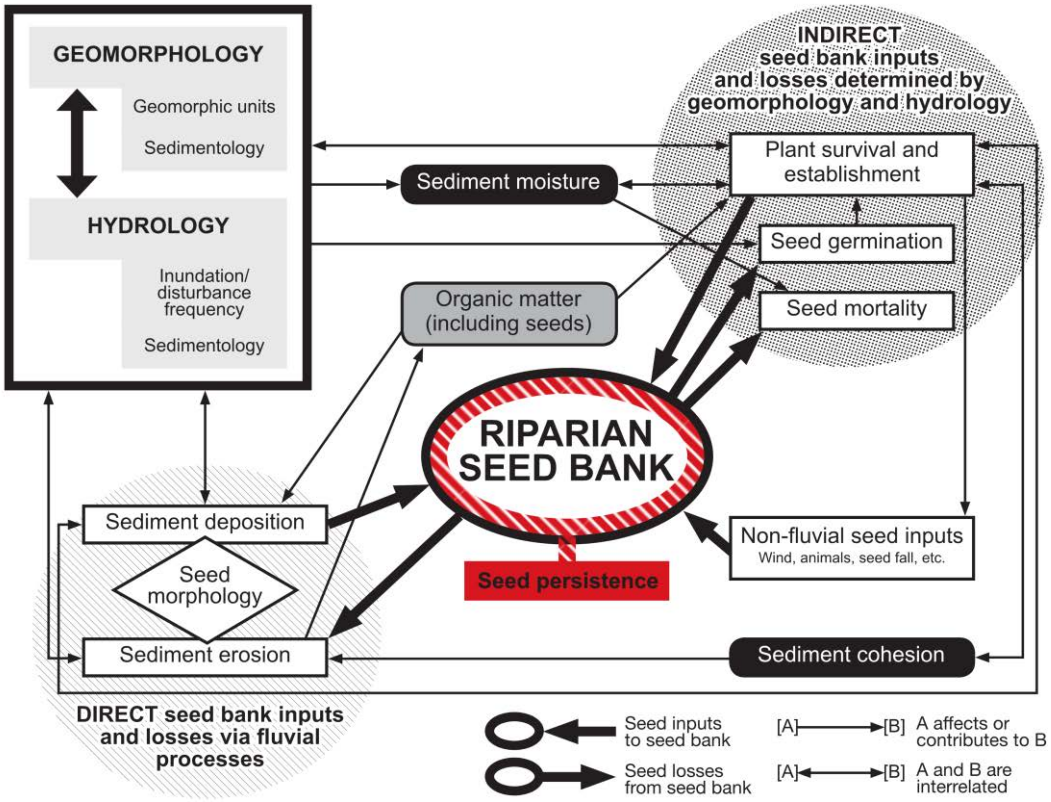
The second important contribution is summarised in Figure 2 (reproduced from chapter 3, Figure 6). It details, for the first time, the one-way and reciprocal

interactions between seed banks, established vegetation, and hydrological and fluvial processes that ultimately determine the composition of the seed bank. The relative influence of each factor on seed bank composition will vary depending on location within the riparian zone and between catchments. Figure 2 captures both the influence of biogeomorphic processes on the composition of the seed bank, and the influence of regeneration from the seed bank on biogeomorphic processes. It is based on both the findings of this thesis and research conducted by others. '*Geomorphology*' and '*Hydrology*' are boxed together indicating their relatedness and combined role as primary drivers in the web of interactions. This is best exemplified by the findings of chapter 2 (described in the preceding section). '*Sedimentology*' is presented as an indicator of both geomorphology (e.g. chapter 3, Figures 2, 3, 4; Fryirs and Brierley 2013) and hydrological influences (Brierley and Fryirs 2005) and was found to reflect seed bank characteristics. In chapter two for example, a weak but significant trend of increasing seed bank abundance with increasing fine particles and decreasing sand and gravel was apparent (chapter 3, Figure 3). Seed bank species richness increased with decreasing particle size and increased with the percentage of organic matter (chapter 3, Figure 4). The general weakness of the observed relationships was considered to relate to variability in bed grain size between the four study reaches (chapter 3, Figure 2). Nevertheless, the findings were consistent with sedimentological qualities observed in other riparian seed bank studies (e.g. Goodson et al. 2003, Gurnell et al. 2008, Oishi et al. 2010).

Figure 2 also represents the role of fluvial processes ('*Sediment erosion*' and '*Sediment deposition')* in contributing to, and removing seeds from seed banks (e.g. seeds

deposited along with sediment, Goodson et al. 2003, Gurnell et al. 2008). '*Sediment cohesion'* is presented as a controlling factor, and linked to '*Plant survival and establishment'*, reflecting the biogeomorphic relationship between the two (Corenblit et al. 2009). Frequent erosion (or sediment reworking) that flushes seeds from non-cohesive sediments will reduce species richness (such as that observed in bar seed banks: chapter 2, Figure 5b), but not necessarily affect seed bank abundance. In chapter two for example, dense populations of *Gratiola peruviana* and *Isolepis inundata* established on two individual bars, contributed thousands of seeds to each respective seed bank, greatly increasing the overall variability of bar seed bank abundance, but not species richness (chapter 2, Figure 4a, b). Subsequently, '*Plant survival and establishment*' also represents these seed contributions to the seed bank from standing vegetation. '*Seed morphology'* is linked to sediment deposition and erosion to acknowledge species-specific responses to fluvial and hydrological processes based on seed morphology (e.g. Cerdà and García-Fayos 2002, Chambert and James 2009, García-Fayos et al. 2010). This is included, despite finding no evidence for fluvial seed sorting at the geomorphic unit scale, as noted in chapter 3 (chapter 3, Figure 5). Recent work by Carthey et al. (in press) however, has shown that seed morphology influences the nature of seed transport and the likelihood of transport via the water surface, within the water column, and with bedload sediments, with implications for seed deposition.

Figure 2 (opposite) – (reproduced from chapter 3 [Figure 6])**.** *Factors contributing to spatial variability in riparian seed banks*: Direct seed bank inputs and losses are influenced by fluvial processes: sediment deposition is the main process by which riparian seed banks form. Seeds are deposited along with sediment, as well as organic matter. Erosion results in the removal of seeds from seed bank sediments and contributes seeds to the general pool of organic matter, from which seeds may be redeposited elsewhere. Species-specific differences in seed morphology such as density and shape introduce complexity to seed responses to fluvial erosion and deposition. Indirect seed bank inputs and losses influenced by geomorphology and hydrology: variations in hydrological factors such as inundation frequency and duration are most clearly observed at the geomorphic unit scale. Hydrological conditions associated with different geomorphic units, are evident in differences in sediment moisture, which will differentially affect seed mortality and germination, both of which result in seed losses from the seed bank. Inundation resulting in sediment disturbance may encourage germination. Hydrology and fluvial processes affect the survival and establishment of seeds that germinate from the seed bank by determining soil/sediment moisture levels and organic matter content. The development of vegetation assemblages increases the cohesion and stability of sediments, reducing the likelihood or extent of erosion and thus seed removal. Plants surviving to reproductive maturity have the capacity to contribute seeds to the seed bank directly, via fluvial processes, or via animals or wind. Non-fluvial seed inputs: These include seeds delivered to seed banks by non-fluvial mechanisms, including wind, animals, and direct seed fall. Parent plants may or may not have established under the influence of fluvial processes. The importance of seed-persistence in determining the final composition of riparian seed banks has been added in red.



The framework outlined in Figure 2 shows the two main pathways by which seeds are contributed to seed banks – hydrochorically transported seeds delivered by the river, and seed rain from local vegetation. The dominance of one pathway over the other is determined by the degree of exposure to water flow and thus position within the channel or floodplain. For example, in chapter four, bar vegetation was comprised of mainly hydrochoric and wind-dispersed species, whereas bench and floodplain vegetation was increasingly represented by non-hydrochorous seed inputs (chapter 4, Figure 6). However, species-specific variability in seed persistence (added to Figure 2 in red) will be an important filter influencing the final composition of the seed bank. Seed bank composition is commonly found to be much less variable than the standing vegetation within riparian ecosystems, due to the dominance of pioneer and early

successional species (e.g. Chapter 4, Figure 3; Hanlon et al. 1998, Webb et al. 2006, Bossuyt and Honnay 2008, Williams et al. 2008).

The findings related to aims 1 & 2 of this thesis contribute a framework for distinguishing areas or features of comparatively high or low seed bank species richness (and to some extent abundance), within river reaches. In the framework, ecosystem attributes related to vegetation density and diversity, sediment grain size and organic content, geomorphic unit type and the complexity of sediment stratification are used as indicators of seed bank characteristics. The ecosystem attributes are easily observed without specialist equipment. The framework should be of use to those aiming to assess relative seed bank species richness, and to some extent abundance, within their rivers, and provide some means for directing seed bank-related activities accordingly. The framework is outlined in Table 1, with the basis for the framework outlined in Figure 3.

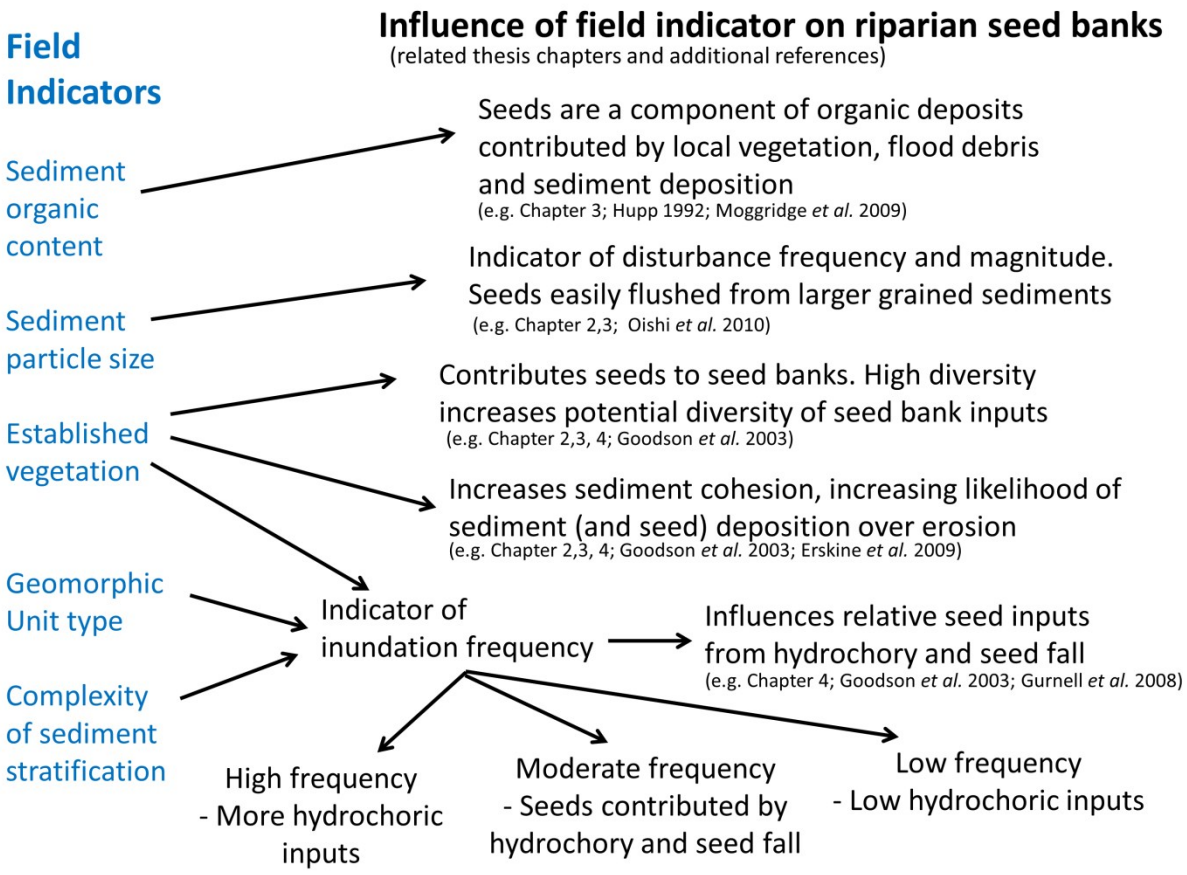


Figure 3 – Framework outlining the influence of five ecosystems attributes on riparian seed banks.

Table 1 – Framework for distinguishing between areas of potentially high and low seed bank species richness and to some extent, abundance within a river reach, based on ecosystem attributes observed in the field.

Features indicating potentially higher species richness and abundance of the seed bank	**Features indicating potentially lower species richness and abundance of the seed bank**
• Higher sediment organic matter content • High percentage of fine sediment particles.	• Low sediment organic matter content • Greater sediment particle size (sand and gravels)
• High diversity of established standing vegetation • Alternating organic and sediment layers (indicator of potentially species rich seed banks) • Intermediate inundation frequency for sediments stabilised by vegetation	• Sparsity of established vegetation • Few discernible sediment layers (indicator of low to moderate species richness) • Frequently inundated surfaces on non-cohesive sediments

THESIS AIM 3: **Potential contribution of the seed bank to riparian vegetation and geomorphic river recovery – an analysis of plant species traits**

Background and research approach

Historically, the potential for seed banks to contribute to ecosystem restoration was evaluated by their similarity to the dominant native vegetation (e.g. Brock and Rogers 1998, Pettit and Froend 2001, Robertson and James 2007, Boudell and Stromberg 2008). Common measures were the number of species in the standing vegetation

represented by the seed bank, and the presence of additional native species not observed in the standing vegetation (e.g. Capon and Brock 2006, Webb et al. 2006). Alternative approaches examined the seed bank in terms of plant species traits such as plant growth form, or habitat tolerances (e.g. stress tolerator vs competitive) (Bornette et al. 2008, Gurnell et al. 2008). This allowed comparison of the structure and ecological function of regenerating assemblages with that of the standing vegetation, without focus on specific species (Biswas and Mallik 2010).

This thesis adopts a novel approach, and investigates the potential role of the seed bank in supporting the geomorphic recovery of river reaches. Plant species traits are used to determine the role of each species in the seed bank in supporting biogeomorphic processes and driving geomorphic change (Hupp 1992, Hupp and Osterkamp 1996, Corenblit et al. 2007). In chapter four, bars, benches and the floodplain are positioned respectively along a trajectory of biogeomorphic succession, based on their geomorphology and associated vegetation (e.g. sparsely vegetated geomorphic units with relatively non-cohesive sediments [bars] tending toward units increasingly stabilised by inrceasingly diverse and later-successional vegetation assemblages [benches and floodplain]; see also Hupp 1992, Hupp and Osterkamp 1996, Bendix and Hupp 2000, van Coller et al. 2000, Corenblit et al. 2007). Plant growth form, longevity (annual vs perennial) and seed dispersal mechanisms - historically traits used to compare the structure of vegetation assemblages or determine likely seed bank seed inputs (e.g. Goodson et al. 2002) - were instead used to provide an indication of each species' likely habitat, response to hydrological forces, influence on geomorphology and tolerance of inundation (Arcement and Schneider

1989, Hupp 1992, Bornette et al. 2008, Biswas and Mallik 2010). For example both annual and perennial plants would contribute to sediment stabilisation through root development (Abernethy and Rutherfurd 1998, Abernethy and Rutherfurd 1999, Simon and Collison 2002). Annual species were considered more likely to successfully colonise bare, frequently inundated sediments than perennial species (Hupp 1992, Stromberg et al. 2010). However, perennial growth forms including woody shrubs and trees were considered to provide greater and more long-term stabilisation (Hupp 1992, Schenk and Jackson 2002, Erskine et al. 2009). Hydrochorically-dispersed species were considered more likely riparian and aquatic or inundation-tolerant to some extent, while animal-dispersed species considered more likely terrestrial and less inundation-tolerant (Johansson et al. 1996, Nilsson et al. 2002). The capacity of the seed bank to support different stages of biogeomorphic succession was assessed by comparing the traits of the species in the seed bank with those of the vegetation assemblages associated with bars, benches and the floodplain.

Relevance and contribution of the findings to international seed bank research

The findings of this thesis broaden the range of contexts under which seed bank-based regeneration may support the recovery or restoration of riparian zones. It is among the first research to consider the influence of regeneration from the seed bank on biogeomorphic processes (e.g. Hupp 1992, Corenblit et al. 2007, Hupp and Rinaldi 2007). The seed bank was found to be dominated by pioneer and early-successional plant species, regardless of the geomorphic unit (chapter 4, Figure 5), or the condition of the river reach (chapter 5, Figure 3), and most resembled the growth forms and composition of vegetation established on bars (chapter 4, Figure 5). Compositional

similarity between the seed bank and standing vegetation is known to be higher in environments where frequent disturbance simultaneously facilitates germination from the seed bank and inhibits plant succession (Hopfensperger 2007). This may well be the case for bars, subjected to frequent inundation and sediment reworking. Pioneer species are the first to colonise frequently disturbed or bare soils and sediments, and can facilitate vegetation succession through the alteration of the local biotic and abiotic environment (Prach et al. 2001). In this context, seed bank based-revegetation could be particularly useful in the regeneration of floodplain vegetation in cleared and degraded river reaches by enhancing the development of groundcover. The seed bank could contribute to natural recruitment, such as that observed by Hough-Snee et al. (2013) following livestock removal from river reaches.

Pioneer species also facilitate the earliest stages of biogeomorphic succession within river channels through the colonisation of non-cohesive and frequently disturbed sediments (Hupp 1992). Developing root systems stabilise sediment and the presence of vegetation can encourage sediment deposition (Abernethy and Rutherfurd 1998, Corenblit et al. 2010). Over time, repeated deposition facilitates the vertical growth of the geomorphic unit and later colonisation by non-pioneer species (e.g. chapter 2; Hupp 1992, Corenblit et al. 2009). For eroded, incised and over-widened river reaches, natural recovery in the form of channel contraction can occur as a result of these processes, as the transition of bars to benches and benches to inset-floodplain reduce the cross-sectional area of the channel over time (Fryirs and Brierley 2000, Erskine et al. 2009, Erskine and Chalmers 2009). Encouraging regeneration from the seed bank in key locations such as elevated (and thus less frequently inundated) bars or recent

sediment deposits upon benches could initiate the stabilisation of these sediments and support the early stages of channel contraction.

Vegetation will differ between catchments depending on factors such as climate, rainfall, hydrological regime and anthropogenic disturbance. However, as the majority of seed banks are dominated by pioneer and early successional species (Hopfensperger 2007, Bossuyt and Honnay 2008), regeneration from the seed bank should be able to contribute to the development of groundcover vegetation, and through regeneration aid the stabilisation of bare sediments in sand and possibly gravel-bed rivers across a range of climates (Hupp 1992, Corenblit et al. 2010, Gurnell et al. 2012). Regeneration success is likely to be greatest in locations that allow seeds to accumulate (such as depositional geomorphic units), with greater uncertainty for frequently inundated non-cohesive sediments, or zones prone to erosion (Berge and Hestmark 1997, Goodson et al. 2002).

This thesis also contributes to our general understanding of the capacity for seed banks to reflect qualities of standing vegetation, and in particular, changes in vegetation associated with riparian degradation. Few studies have attempted to compare seed banks between different condition reaches within the same catchment, despite the information this provides on the processes by which seed banks might contribute to, or buffer, continuing riparian degradation (Williams et al. 2008). In chapter five, seed banks were found to reflect the terrestrialisation of the standing vegetation which is commonly associated with declines in riparian condition and the encroachment of exotic species (Nilsson et al. 1991a, Catford et al. 2011). For example,

the proportion of exotic species in the standing vegetation and seed bank increased from good to poor condition reaches (chapter 5, Figure 2b). Associated with increasing proportions of exotic species was a shift in the seed bank from native riparian herbs, sedges and rushes, to more terrestrial exotic herbs and grasses (chapter 5, Figure 3c). These changes associated with riparian condition have implications for the "quality" or suitability of seeds available in the seed bank for river restoration activities. The encouragement of exotic species contradicts common goals of ecosystem management and restoration, which generally aim to increase native biodiversity and remove or control exotic and invasive species (e.g. Holmes et al. 2005, Shafroth et al. 2005, Brooks and Lake 2007). Secondly, the altered conditions associated with riparian degradation, and the limited abundance of strictly riparian plant propagules in the seed bank reduce the capacity for the seed banks to contribute to the regeneration of dominantly native *riparian* plant communities. Whilst each catchment reflects its own history of modification and the capacity of its rivers to adjust, the encroachment of exotic species and the terrestrialisation of vegetation are a common feature of regulated and degraded rivers, with likely implications for the composition and utility of seed banks (Nilsson et al. 1991a, Catford et al. 2011, Greet et al. 2012).

THESIS AIM 4: **Implications for the use of seed bank-based revegetation to support river management and restoration goals**

The final component of this thesis aimed to determine the extent to which riparian seed banks could be better utilised in river management and restoration. The primary focus of this thesis has been on how revegetation from seed banks can be used to

enhance geomorphic recovery. However, other benefits of re-establishing riparian vegetation include improving the aesthetic value of rivers, improving water quality, regulating water temperature, and providing habitat for a diverse array of terrestrial and aquatic organisms (Howell et al. 1994, Abernethy and Rutherfurd 1998, Tabacchi et al. 1998, Webb et al. 1999, Erskine and Webb 2003, Kelly et al. 2007, Dosskey et al. 2010). The findings of this thesis raise a number of important positive and negative implications for seed bank-based revegetation in river management and restoration, which are presented below. I finish by highlighting two important directions for future seed bank research.

- *There are benefits in using seed bank-based regeneration as a passive approach to revegetation of riparian corridors*

  Natural vegetation recruitment is recognised as an important passive approach to revegetation that supports the recovery of riparian zones (Kauffman et al. 1997, Hough-Snee et al. 2013, Ruwanza et al. 2013). The seasonal recruitment of transient-seeded species could be augmented by seed bank-based regeneration, and increase the diversity of regenerating species. The results of this thesis and other riparian seed bank studies show that riparian seed banks are potentially abundant, and in particular locations species-rich (e.g. in zones which accumulate organic matter and sediment). Small volumes of sediment may hold hundreds or thousands of propagules (e.g. chapter 2, Figure 3). The majority of these are likely to be herbaceous or pioneer species, which are capable of establishing within a diverse array of conditions and environments (Middleton 2003, Hopfensperger 2007, Bossuyt and Honnay 2008). Three important benefits of seed banks as a

passive approach to revegetation are 1) their cost of acquisition (nothing), 2) the fact that the seeds come pre-selected, and 3) that the seeds are already in place. Alternative active approaches for reintroducing pioneer vegetation within the riparian zone such as direct seeding, involves selecting desirable species, collecting or purchasing seed stocks and ultimately planting those seeds in desired locations (e.g. Schneider 2007, Ruwanza et al. 2013). The successful establishment of plants from either approach is dependent on the prevailing environmental conditions (Ruwanza et al. 2013). In this sense, seed banks have the advantage of being more diverse than the seed mixes selected for direct seeding, and thus they are more likely to contain different species able to establish under a range of different conditions (Casanova and Brock 2000, Ogden et al. 2002, Capon 2007).

- *Seed-bank based revegetation will need to be combined with other revegetation approaches to achieve wider goals related to riparian management and river restoration.*

  Riparian vegetation is described as a patch mosaic of different successional stages, associated with a diverse array of different geomorphic features (Harris 1987, van Coller et al. 2000, Richardson et al. 2007). Seed banks can clearly contribute to the regeneration of herbs and early successional vegetation, but are less reliable for the regeneration of woody shrubs, trees and also vines (chapter 4, Table 1; chapter 5, Table 6; Hopfensperger 2007). This thesis research highlighted the role that the passive regeneration of early successional species such as herbs, sedges, rushes and grasses from seed banks may play in geomorphic river recovery by initiating or supporting biogeomorphic channel contraction processes through sediment stabilisation (chapters 4 and 5). These species can also provide important

ecosystem services, such as the maintenance of water quality and provision of aquatic habitat (Hupp 1992, Bunn et al. 1999, Dosskey et al. 2010). However, shrubs and especially trees contribute another set of ecological services including the provision of habitat for a range of different fauna (particularly fish), shading and water temperature control, river bank stabilisation and the contribution of woody debris to river channels (Osborne and Kovacic 1993, Howell et al. 1994, Abernethy and Rutherfurd 1998, Tabacchi et al. 1998, Webb et al. 1999, Erskine and Webb 2003, Kelly et al. 2007). Active revegetation methods such as direct-seeding and tube stock planting will be required to reestablish these growth forms and other desirable species known to be in low numbers or completely absent from the seed bank. The decision to embark on passive or active management restoration approaches, or a combination of the two depends on a number of factors including the nature of river degradation and its causes, and the availability of resources to support management or restoration activities (McIver and Starr 2001).

- *Riparian degradation affects the capacity for seed bank-based regeneration to contribute to native riparian vegetation*

  A significant challenge for river management is associated with re-establishing *riparian* vegetation within river reaches for which the hydrological regime and/or geomorphic structure has been substantially altered. Many anthropogenic pressures on rivers, and the geomorphic adjustments that occur in response to them, effectively reduce water availability for plants (Amoros and Bornette 2002, Thoms 2003). River regulation and water extraction for activities such as agriculture

serve to lower the magnitude and frequency of floods and reduce baseflow (Nilsson and Berggren 2000). The clearing of riparian vegetation can serve to destabilize sediments and result in erosion of river channels during higher flows (Prosser et al. 2001). The resulting expansion of the channel can decrease connection between the floodplain and channel, again reducing water availability for plants (Amoros and Bornette 2002, Thoms 2003). Under these conditions, terrestrial plants ill-adapted to frequent inundation, and fast growing exotic species, can often outcompete the riparian plant species that dominated before disturbance (Jensen et al. 2008, Williams et al. 2008, Catford et al. 2011). This thesis research suggests that the changes in vegetation associated with anthropogenic disturbance and related geomorphic adjustments are easily transferred to the seed bank (chapter 5), and this ultimately affects the capacity for the seed bank to contribute to the regeneration of native riparian vegetation. The allocation of environmental flows is an example of extreme intervention that could potentially aid the reestablishment of riparian vegetation communities from seed banks along regulated rivers, however the impacts of such changes on exotic species richness are unclear (Pettit et al. 2001, Catford et al. 2011, Reid and Capon 2011).

- *The regeneration of exotic species will need to be controlled to maximize the benefits of seed bank-based revegetation in riparian corridors*

  Native propagules do reside in the seed banks of even highly degraded river reaches (e.g. chapter 5 Figures 2a, 3a, b). However, exotic species dominate the seed banks of highly degraded river reaches, lowering the likelihood of native species regenerating (e.g. DA reach, chapter 5, Figure 3a; Ruwanza et al. 2013). There are a range of management actions that may be applied to encourage the regeneration

and establishment success of native species in the seed bank, and controlling invasive or exotic species (Randall 1996). The findings of this thesis suggest that the effort expended will need to increase with the degree of riparian degradation. The successful eradication of all exotic species is in most cases an unrealistic goal (Loope et al. 1988, Ewel and Putz 2004). However efforts may focus simply on removing invasive and selected exotic species that regenerate from the seed bank through weed management programs (e.g. Northern Territory Government 2014, Peachey 2015).

- *Highly degraded river reaches should be used to demonstrate the benefits of seed bank-based revegetation.*

  Resources for supporting the re-establishment of riparian vegetation as part of river management and restoration activities are limited, and understandably directed at river reaches for which there exists some promise for recovery (Harris and Olson 1997, Roni et al. 2002). Significant effort may be required to control exotic species regenerating from the seed bank in even moderately degraded river reaches. As such, the greatest benefits for effort expended may be achieved by the use of seed bank-based revegetation in river reaches considered too degraded for restoration efforts to be economically feasible (e.g. Booth and Jackson 1997), with no significant follow-up management. Reaches cleared of canopy and understory species, and eroded and degraded reaches from which livestock has been excluded are examples of potential test reaches (e.g. Kauffman and Krueger 1984, Sarr 2002, Hough-Snee et al. 2013). The benefit of conducting rehabilitation in such degraded reaches, is that seed bank-based regeneration is unlikely to contribute to further

degradation of the reach. At these sites, regeneration of what may be considered undesirable species in good condition reaches (e.g. exotic grasses), may provide some essential ecosystem services, such as the provision of habitat or increasing the stability of channel and floodplain sediments (Kauffman et al. 1997). There exists the possibility that over time, the establishment of these species may improve conditions for the natural recruitment of other more desirable species (Hough-Snee et al. 2013). Periodic monitoring of vegetation and geomorphic change could provide invaluable information as to whether seed bank regeneration can contribute to positive changes in vegetation composition and geomorphic stability over time.

Caveats

I acknowledge that the methods I have used to detect species in the standing vegetation (vegetation survey) and seed bank (seedling emergence studies) are likely to provide only a conservative assessment of the true species diversity of each. Additional species would undoubtedly be detected given an increase in sampling effort. Similarly, the use of a single watering treatment for the seedling emeergence studies may have impeded the germination of species requiring different moisture levels for germination and survival (e.g. aquatic species, see Casanova and Brock 2000, Capon 2007). It would be also be remiss to assume all seeds detected in the seedling emergence studies (Appendices 4 and 5) were part of the true persistent soil seed bank. Leaf litter contains persistent *and* transient seeds (short-lived seeds that do not become part of the persistent seed bank), and in most cases some leaf litter was incorporated into the sediment samples collected for this research. *Ficus coronata*

seeds for example were present in particular samples collected close to established trees and may be transient species. In contrast, *Juncus* species, which were present in the majority of samples, are known to be persistent and are thus likely to to be a component of the true persistent seed bank (Bossuyt and Honnay 2008).

It should also be acknowledged that "slice in time" surveys, such as a single vegetation survey or seedling emergence trial, fail to capture important changes in vegetation and seed bank composition that occur over time (e.g. Gurnell 2007). However, the focus of this thesis is on patterns of plants *traits* for the species found in the seed bank and standing vegetation, as opposed to an anaysis of specific species composition (or compositional turnover). This thesis does not attempt to establish causal or temporal relationships between the seed bank and standing vegetation, or between these factors and antecedent conditions.

Important future directions in seed bank research

Currently there is a disjunct between our conceptualisation of *potential* for the regeneration of vegetation from the seed bank and actually encouraging germination and regeneration from seed banks *in situ.* Clearly the next important area of riparian seed bank research should be directed toward investigating the types of disturbance that could be applied in the field to enhance the germination of the seed bank. Glasshouse trials have shown many seeds require little more than disturbance, light and some degree of moisture for germination to be encouraged (Gurnell et al. 2007b, Price et al. 2010). Field-based plot trials could be established on a range of geomorphic

surfaces for which the regeneration of vegetation is considered desirable. Such locations could include cleared, degraded floodplains, bare sediments such as recent flood deposits, bars, unvegetated benches, and strategic locations on sediment slugs. A range of manipulation experiments should be trialled to test their success in germinating seeds that may be dormant, or to improve the success rate of seed bank germination. One such approach would be the simple mechanical disturbance (e.g. raking) of the top 5 cm of sediment or soil, possibly in combination with regular watering (Ruwanza et al. 2013). An alternative approach for more densely vegetated locations would be to facilitate seed bank regeneration through the removal of exotic species in experimental plots. This approach has been applied in some environments with mixed success (e.g. Vosse et al. 2008). The establishment of control plots would allow comparison of plant recruitment rates and final species composition for unassisted plant recruitment and plant recruitment augmented by seed bank manipulation.

A second important area of future research is investigating how to germinate seeds in a seed bank that display prolonged dormancy (Merritt et al. 2007). Seed bank assays using the seedling emergence method are efficient but often fail to detect those species whose seeds require germination cues that are not provided under glasshouse conditions (Gross 1990, Price et al. 2010). Such examples include specific temperature changes, fire, time for after-ripening, chemical cues, scarification etc. (Baskin and Baskin 2004). Some shrubs and trees, which are considered to be lacking from seed banks, display these qualities (Merritt et al. 2007). Initially it would be useful to investigate the proportion of the seed bank that was not readily germinable within a

range of different riparian ecosystems. By combining seedling emergence and floatation extraction techniques, a clearer idea of both the germinable and dormant component of the seed bank may be assessed (Price et al. 2010). This avenue of research would provide the foundations for determining the relative worth of the next phase of research – techniques to break dormancy and enhance germination in riparian seed banks. These could be trialed within laboratories and glasshouses with the aim of ultimately testing these methods at larger scales in the field.

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APPENDICES

GUIDE TO APPENDICES

Appendix 1 - "Supporting information (Table S1)" for O'Donnell et al 2014

This appendix contains the supporting information for O'Donnell et al 2014 (chapter 2). It lists the species identified from the seedling emergence study, with details on each species' family, origin, longevity and growth form.

Appendix 2 – Results of sediment analyses

This appendix contains the results of the sediment analyses that were conducted for chapter three.

Appendix 3 – Species trait data and information sources

This appendix relates to the species trait information that was used to some extent in all four data chapters, but primarily in chapters four and five. Part A includes a list of all plant species identified during the course of this thesis research and acknowledges in which study or survey the species was identified (each seedling emergence study and the vegetation survey). For each species, available data for the species origin, family, growth form, longevity, seed mass, seed length, seed width and mode of seed dispersal are presented. Part B indicates for each species, the internet resources and databases, and published resources used to obtain the trait data in Part A. Internet resources and databases are indicated by abbreviations, which are explained in Part C. References for the published resources cited in Part B are provided in Part D.

Appendix 4 – Results of seedling emergence study 1

This appendix contains the results of the seedling emergence study that commenced in May 2011 and relates to chapters two, three and four. The data (too extensive for reproduction here) is available to view as both a comma separated value file (.csv) or Microsoft Excel file (.xslx) via the following links.

Link to .csv file:

https://drive.google.com/open?id=0Byfdvrg9IkecY0J2U2xJU296RUk

Link to .xslx file:

https://drive.google.com/open?id=0Byfdvrg9IkecV1pPZ0xlemhZaUk

Appendix 5 – Results of seedling emergence study 2

This appendix contains a link to the results of the seedling emergence study that commenced in November 2011, and relates to chapter five. The data (too extensive for reproduction here) is available to view as both a comma separated value file (.csv) or Microsoft Excel file (.xslx) via the links below.

Link to .csv file:

https://drive.google.com/open?id=0Byfdvrg9IkecOV9JSnJMM3N0czg

Link to .xslx file:

https://drive.google.com/file/d/0Byfdvrg9IkecNDhJSGYzNVNpVlk/view?usp=sharing

Appendix 6 – Vegetation survey results

This appendix contains the results of the vegetation survey of the seven study reaches in the Wollombi sub-catchment conducted in October 2011. Additional species identified in the follow up survey in April 2013 are integrated. This data relates to chapters three, four and five. The data (too extensive for reproduction here) is available to view as both a comma separated value file (.csv) or Microsoft Excel file (.xslx) via the links below.

Link to .csv file:

https://drive.google.com/file/d/0Byfdvrg9IkecZU5TYWZCSy1uWlk/view?usp=sharing

Link to .xslx file:

https://drive.google.com/file/d/0Byfdvrg9IkecM3RWdjVid0NENms/view?usp=sharing

Appendix 7 – Supplementary information tables for O'Donnell et al 2016

This appendix contains supplementary information tables for O'Donnell et al 2016 (chapter 5), relating to the determination of river condition.

APPENDIX 1

"Supporting information (Table S1)" for O'Donnell et al 2014 (Chapter 2)

APPENDIX 1 – "Supporting information (Table S1)" for O'Donnell et al 2014

List of species identified from the seedling emergence study in chapter two, with details on each species' family, origin, longevity and growth form.

Family	Scientific name	Origin	Longevity	Growth form
Acanthaceae	*Pseuderanthemum variabile*	Native	Perennial	Herb
Apiaceae	*Centella asiatica*	Native	Perennial	Herb
Apiaceae	*Daucus glochidiatus*	Native	Annual	Herb
Apiaceae	*Hydrocotyle peduncularis*	Native	Annual/Perennial	Herb
Apiaceae	*Hydrocotyle tripartita*	Native	Perennial	Herb
Asteraceae	*Centipeda minima*	Native	Annual	Herb
Asteraceae	*Cineraria lyratiformis*	Exotic	Annual	Herb
Asteraceae	*Conyza parva*	Exotic	Annual	Herb
Asteraceae	*Conyza sumatrensis*	Exotic	Annual	Herb
Asteraceae	*Cotula australis*	Native	Annual	Herb
Asteraceae	*Euchiton sphaericus*	Exotic	Annual	Herb
Asteraceae	*Euchiton gymnocephalus*	Native	Perennial	Herb
Asteraceae	*Gamochaeta americana*	Exotic	Annual	Herb
Asteraceae	*Gamochaeta calviceps*	Exotic	Annual	Herb
Asteraceae	*Hypochoeris radicata*	Exotic	Perennial	Herb
Asteraceae	*Ozothamnus diosmifolius*	Native	Perennial	Shrub
Asteraceae	*Senecio madagascariansis*	Exotic	Annual/Biennial	Herb
Asteraceae	*Senecio minimus*	Native	Annual	Herb
Asteraceae	*Sigesbeckia orientalis*	Native	Annual	Herb
Asteraceae	*Soliva spp.*	Exotic	Annual	Herb
Blechnaceae	*Doodia aspera*	Native	Perennial	Fern
Blechnaceae	*Doodia caudata*	Native	Perennial	Fern
Boraginaceae	*Austrocynoglossum latifolium*	Native	Perennial	Herb
Campanulaceae	*Wahlenbergia communis*	Native	Perennial	Herb
Campanulaceae	*Wahlenbergia gracilis*	Native	Perennial	Herb
Caryophyllaceae	*Cerastium glomeratum*	Exotic	Annual	Herb
Caryophyllaceae	*Stellaria media*	Exotic	Annual/Biennial	Herb
Chenopodiaceae	*Einadia hastata*	Native	Perennial	Shrub
Clusiaceae	*Hypericum gramineum*	Native	Perennial	Herb
Clusiaceae	*Hypericum japonicum*	Native	Annual/Perennial	Herb
Commelinaceae	*Commelina cyanea*	Native	Perennial	Herb
Commelinaceae	*Tradescantia fluminensis*	Exotic	Perennial	Herb
Convolvulaceae	*Dichondra repens*	Native	Perennial	Herb
Cunoniaceae	*Callicoma serratifolia*	Native	Perennial	Tree
Cyperaceae	*Carex inversa*	Native	Perennial	Sedge
Cyperaceae	*Carex maculata*	Native	Perennial	Sedge
Cyperaceae	*Cyperus brevifolius*	Exotic	Perennial	Sedge

Continued…

Family	Scientific name	Origin	Longevity	Growth form
Cyperaceae	*Cyperus difformis*	Native	Annual	Sedge
Cyperaceae	*Cyperus eragrostis*	Exotic	Perennial	Sedge
Cyperaceae	*Cyperus flavescens*	Exotic	Annual	Sedge
Cyperaceae	*Cyperus flavidus*	Exotic	Annual/Perennial	Sedge
Cyperaceae	*Cyperus gracilis*	Native	Perennial	Sedge
Cyperaceae	*Cyperus laevis*	Exotic	Perennial	Sedge
Cyperaceae	*Cyperus polystachyos*	Native	Annual/Perennial	Sedge
Cyperaceae	*Cyperus sanguinolentus*	Native	Annual/Perennial	Sedge
Cyperaceae	*Cyperus sesquiflorus*	Exotic	Annual/Perennial	Sedge
Cyperaceae	*Cyperus tetraphyllus*	Native	Perennial	Sedge
Cyperaceae	*Cyperus trinervis*	Native	Perennial	Sedge
Cyperaceae	*Fimbristylis dichotoma*	Native	Perennial	Sedge
Cyperaceae	*Isolepis inundata*	Native	Perennial	Rush
Cyperaceae	*Isolepis prolifera*	Exotic	Perennial	Rush
Cyperaceae	*Lepidosperma limicola*	Native	Perennial	Sedge
Davalliaceae	*Davallia solida var. pyxidata*	Native	Perennial	Fern
Dicksoniaceae	*Calochlaena dubia*	Native	Perennial	Fern
Elatinaceae	*Elatine gratioloides*	Native	Annual	Aquatic Herb
Euphorbiaceae	*Homalanthus populifolius*	Native	Perennial	Shrub/Tree
Fabaceae	*Trifolium arvense*	Exotic	Annual	Herb
Fabaceae	*Trifolium glomeratum*	Exotic	Annual	Herb
Fabaceae	*Trifolium repens*	Exotic	Perennial	Herb
Gentianaceae	*Centaurium tenuiflorum*	Exotic	Annual	Herb
Geraniaceae	*Geranium homeanum*	Native	Annual/Perennial	Herb
Iridaceae	*Sisyrinchium spp. A*	Exotic	Annual	Herb
Juncaceae	*Juncus articulatus*	Exotic	Perennial	Rush
Juncaceae	*Juncus bufonius* (clustered)	Native	Annual	Rush
Juncaceae	*Juncus bufonius* (solitary)	Native	Annual	Rush
Juncaceae	*Juncus capillaceus*	Exotic	Perennial	Rush
Juncaceae	*Juncus cognatus*	Exotic	Perennial	Rush
Juncaceae	*Juncus continuus*	Native	Perennial	Rush
Juncaceae	*Juncus effusus*	Exotic	Perennial	Rush
Juncaceae	*Juncus fockei*	Native	Perennial	Rush
Juncaceae	*Juncus homalocaulis*	Native	Perennial	Rush
Juncaceae	*Juncus planifolius*	Native	Annual or Perennial	Rush
Juncaceae	*Juncus prismatocarpus*	Native	Perennial	Rush
Juncaceae	*Juncus spp.*	.	.	Rush
Juncaceae	*Juncus usitatus*	Native	Perennial	Rush
Lobeliaceae	*Lobelia anceps*	Native	Perennial	Herb
Lobeliaceae	*Pratia purpurascens*	Native	Perennial	Herb
Lomandraceae	*Lomandra longifolia*	Native	Perennial	Herb

Continued…

Family	Scientific name	Origin	Longevity	Growth form
Malvaceae	*Sida rhombifolia*	Exotic	Perennial	Subshrub
Mimosoideae	*Acacia spp.*	Native	Perennial	Tree
Moraceae	*Ficus coronataa*	Native	Perennial	Shrub/Tree
Myrtaceae	*Eucalyptus spp*	Native	Perennial	Tree
Myrtaceae	*Eucalytpus amplifolia*	Native	Perennial	Tree
Onagraceae	*Oenothera spp.*	Exotic	Annual or Perennial	Herb
Oxalidaceae	*Oxalis perennans*	Native	Perennial	Herb
Philydraceae	*Philydrum lanuginosum*	Native	Perennial	Aquatic Herb
Phytolaccaceae	*Phytolacca octandra*	Exotic	Short-lived Perennial	Woody Herb
Plantaginaceae	*Plantago lanceolata*	Exotic	Annual/Biennial	Herb
Plantagincaeae	*Veronica persica*	Native	Annual	Herb
Plantagincaeae	*Veronica plebeia*	Native	Perennial	Herb
Poaceae	*Axonopus fissifolius*	Axotic	Perennial	Grass
Poaceae	*Briza minor*	Exotic	Annual	Grass
Poaceae	*Cynodon dactylon*	Exotic	Perennial	Grass
Poaceae	*Digitaria ciliaris*	Exotic	Annual	Grass
Poaceae	*Echinopogon ovatus*	Native	Perennial	Grass
Poaceae	*Ehrharta erecta*	Exotic	Perennial	Grass
Poaceae	*Entolasia marginata*	Native	Perennial	Grass
Poaceae	*Entolasia stricta*	Native	Perennial	Grass
Poaceae	*Microlaena stipoides*	Native	Perennial	Grass
Poaceae	*Oplismenus imbecillis*	Native	Perennial	Grass
Poaceae	*Oplismenus aemulus*	Native	Perennial	Grass
Poaceae	*Poa annua*	Exotic	Annual	Grass
Poaceae	*Setaria gracilis*	Exotic	Perennial	Grass
Poaceae	*Setaria parviflora*	Exotic	Perennial	Grass
Poaceae	*Vulpia myuros*	Exotic	Annual	Grass
Polygonaceae	*Persicaria decipiens*	Native	Perennial	Herb
Polygonaceae	*Persicaria lapathifolia*	Native	Perennial	Herb
Polygonaceae	*Persicaria strigosa*	Native	Perennial	Herb
Polygonaceae	*Acetosella vulgaris*	Exotic	Perennial	Herb
Primulaceae	*Anagallis arvensis*	Exotic	Annual	Herb
Pteridaceae	*Adiantum aethiopicum*	Native	Perennial	Fern
Pteridaceae	*Adiantum formosum*	Native	Perennial	Fern
Pteridaceae	*Cheilanthes sieberi subsp. sieberi*	Native	Perennial	Fern
Pteridaceae	*Pteris tremula*	Native	Perennial	Fern
Ranunculaceae	*Clematis aristata*	Native	Perennial	Woody Vine
Rosaceae	*Rubus parvifolius*	Native	Perennial	Shrub/Climber
Rosaceae	*Rubus rosifolius*	Native	Perennial	Shrub
Rosaceae	*Rubus moluccanus var. trilobus*	Native	Perennial	Shrub/Climber
Rubiaceae	*Morinda jasminoides*	Native	Perennial	Shrub/Climber

Continued…

Family	Scientific name	Origin	Longevity	Growth form
Scrophulariaceae	*Gratiola peruviana*	Native	Perennial	Herb
Solanaceae	*Solanum americanum*	Native	Annual/Perennial	Woody Herb
Solanaceae	*Solanum aviculare*	Native	Perennial	Shrub
Solanaceae	*Solanum linnaeum*	Exotic	Perennial	Shrub
Solanaceae	*Solanum nigrum*	Exotic	Annual/Perennial	Woody Herb
Ulmaceae	*Trema tomentosa*	Native	Perennial	Shrub/Tree
Verbenaceae	*Verbena bonariensis*	Exotic	Annual/ Perennial	Herb
Violaceae	*Viola hederacea*	Native	Perennial	Herb
Vitaceae	*Cissus hypoglauca*	Native	Perennial	Woody Vine

APPENDIX 2

Results of sediment analyses (Chapter 3)

APPENDIX 2 – Results of sediment analyses (Chapter 3)

Weight (g) not including organic component

		Site / Geomorphic unit / unit replicate no.					
Fraction	Aggregate name	WSF	WSF	WSF	WSF	WSF	WSF
>4mm		171.24	0.00	53.48	0.00	1.11	8.40
2.8-4mm	gravel	58.73	0.00	3.65	0.00	0.53	3.38
2-2.8mm		53.69	0.00	3.96	0.00	0.58	4.08
1.4-2mm		46.55	0.93	7.76	0.69	3.54	3.90
1-1.4mm		41.97	4.39	12.56	2.15	5.15	2.67
710-1000 µm		42.14	9.24	21.52	5.26	13.73	5.37
500-710 µm		64.44	43.46	53.90	31.36	43.33	19.00
355-500 µm	sand	66.10	101.98	98.39	87.46	80.68	78.54
250-355 µm		44.44	101.07	87.87	94.94	62.70	107.08
180-250 µm		18.42	42.63	46.73	48.47	31.44	68.71
125-180 µm		7.54	15.45	22.61	20.14	13.46	29.37
90-125 µm		2.72	5.00	10.14	6.70	4.95	9.03
63-90 µm		1.53	2.71	7.86	3.28	2.52	4.02
<63 µm	fines (silt & clay)	2.53	4.65	16.61	4.63	3.49	4.00
	% gravel	45.60%	0.00%	13.67%	0.00%	0.83%	4.56%
	% sand	53.99%	98.60%	82.62%	98.48%	97.86%	94.29%
	% fines	0.41%	1.40%	3.72%	1.52%	1.31%	1.15%

		Site / Geomorphic unit / unit replicate no.					
Fraction	Aggregate name	WSF	WSF	WSF	UW	UW	UW
>4mm		0.00	0.61	0.00	1.43	0.00	0.02
2.8-4mm	gravel	0.00	0.00	0.00	0.58	0.00	0.08
2-2.8mm		0.00	0.08	0.00	1.45	0.00	0.81
1.4-2mm		0.00	0.28	0.07	1.01	0.00	2.09
1-1.4mm		0.12	0.49	0.20	3.07	0.11	4.54
710-1000 µm		0.29	0.94	0.49	3.90	3.87	12.23
500-710 µm		1.56	1.72	1.49	9.13	23.01	55.78
355-500 µm	sand	6.00	5.42	4.79	36.18	144.08	171.42
250-355 µm		15.31	16.96	14.39	147.19	216.96	162.20
180-250 µm		16.93	22.34	19.51	160.60	100.70	36.44
125-180 µm		10.60	20.86	14.10	65.59	26.17	7.17
90-125 µm		4.12	12.77	6.13	17.04	6.08	2.21
63-90 µm		2.11	7.35	3.21	7.89	2.87	1.38
<63 µm	fines (silt & clay)	11.16	16.07	19.76	12.55	3.20	2.55
	% gravel	0.00%	0.65%	0.00%	0.74%	0.00%	0.20%
	% sand	83.63%	84.18%	76.51%	96.58%	99.39%	99.25%
	% fines	16.37%	15.18%	23.49%	2.68%	0.61%	0.56%

APPENDIX 2 – Results of sediment analyses (Chapter 3)

Weight (g) not including organic component

		Site / Geomorphic unit / unit replicate no.					
Fraction	Aggregate name	UW	UW	UW	UW	UW	UW
>4mm		0.00	0.00	0.00	0.00	0.00	0.00
2.8-4mm	gravel	0.00	0.00	0.00	0.00	0.00	0.00
2-2.8mm		0.00	0.00	0.00	0.00	0.00	0.00
1.4-2mm		0.00	0.38	0.00	0.00	0.06	0.00
1-1.4mm		0.45	0.60	0.28	0.17	0.23	0.04
710-1000 µm		0.82	1.26	4.43	0.28	0.33	0.16
500-710 µm		4.11	8.84	7.27	0.54	1.19	1.62
355-500 µm	sand	33.60	73.97	39.36	1.85	8.68	11.46
250-355 µm		133.45	159.65	132.74	8.96	31.67	32.93
180-250 µm		131.74	121.36	130.23	16.84	28.27	28.42
125-180 µm		60.95	34.69	48.80	17.34	14.46	14.81
90-125 µm		17.43	8.24	15.87	10.84	8.63	6.18
63-90 µm		7.69	2.93	7.91	6.74	6.11	3.40
<63 µm	fines (silt & clay)	6.65	2.30	8.40	21.60	20.72	7.62
	% gravel	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
	% sand	98.32%	99.44%	97.87%	74.64%	82.78%	92.85%
	% fines	1.68%	0.56%	2.13%	25.36%	17.22%	7.15%

		Site / Geomorphic unit / unit replicate no.					
Fraction	Aggregate name	WOW	WOW	WOW	WOW	WOW	WOW
>4mm		10.66	36.63	16.43	51.67	0.00	0.00
2.8-4mm	gravel	6.88	13.92	11.18	17.97	0.41	0.00
2-2.8mm		5.74	19.02	22.45	26.30	1.05	0.00
1.4-2mm		6.60	30.89	49.98	44.51	1.46	0.08
1-1.4mm		13.65	51.32	88.95	76.59	1.59	0.10
710-1000 µm		30.62	70.98	105.85	97.43	3.79	0.45
500-710 µm		64.29	102.31	142.31	101.67	27.04	1.30
355-500 µm	sand	81.77	113.84	151.93	75.81	102.35	21.76
250-355 µm		62.42	80.56	103.58	59.25	157.31	39.03
180-250 µm		26.05	28.00	40.04	25.75	123.38	45.79
125-180 µm		9.07	8.72	13.70	8.92	55.32	30.65
90-125 µm		3.17	2.64	4.47	2.76	17.02	14.70
63-90 µm		1.71	1.27	2.18	1.32	8.26	9.49
<63 µm	fines (silt & clay)	2.20	1.80	2.87	1.75	14.58	15.94
	% gravel	7.17%	12.38%	6.62%	16.21%	0.28%	0.00%
	% sand	92.16%	87.30%	93.00%	83.49%	96.88%	91.11%
	% fines	0.68%	0.32%	0.38%	0.30%	2.84%	8.89%

APPENDIX 2 – Results of sediment analyses (Chapter 3)

Weight (g) not including organic component

		Site / Geomorphic unit / unit replicate no.					
Fraction	Aggregate name	WOW	WOW	WOW	L	L	L
>4mm		0.00	0.00	0.00	0.00	0.00	0.00
2.8-4mm	gravel	0.00	0.07	0.00	0.00	0.00	0.45
2-2.8mm		0.00	0.00	0.01	0.00	0.07	0.87
1.4-2mm		0.00	0.17	0.14	0.00	0.14	3.20
1-1.4mm		0.09	0.18	0.25	0.93	1.10	8.40
710-1000 µm		0.30	0.50	0.56	3.15	7.27	20.69
500-710 µm		1.39	1.23	1.07	29.11	65.96	102.85
355-500 µm	sand	6.62	5.74	3.26	236.20	278.93	289.57
250-355 µm		22.57	18.32	12.23	321.19	227.61	200.24
180-250 µm		28.64	20.43	21.97	92.51	32.76	31.11
125-180 µm		17.12	18.11	23.05	19.02	7.85	1.81
90-125 µm		6.42	10.21	12.36	6.27	1.85	0.37
63-90 µm		3.10	5.68	6.65	2.86	0.67	0.21
<63 µm	fines (silt & clay)	53.78	35.07	41.58	4.20	0.68	0.42
	% gravel	0.00%	0.06%	0.01%	0.00%	0.01%	0.20%
	% sand	61.59%	69.63%	66.22%	99.41%	99.88%	99.74%
	% fines	38.41%	30.31%	33.77%	0.59%	0.11%	0.06%

		Site / Geomorphic unit / unit replicate no.					
Fraction	Aggregate name	L	L	L	L	L	L
>4mm		0.00	0.00	0.00	0.00	0.25	0.00
2.8-4mm	gravel	0.00	0.00	0.00	0.00	0.00	0.00
2-2.8mm		0.02	0.02	0.00	0.00	0.00	0.00
1.4-2mm		0.07	0.12	0.00	0.00	0.07	0.00
1-1.4mm		0.10	0.18	0.08	0.08	0.04	0.00
710-1000 µm		0.20	0.70	0.29	0.17	0.05	0.04
500-710 µm		1.96	27.77	5.54	0.33	0.20	0.17
355-500 µm	sand	59.28	197.35	100.27	2.92	0.55	2.40
250-355 µm		218.61	121.50	393.34	23.71	1.61	26.24
180-250 µm		146.59	42.04	209.27	36.75	3.85	46.24
125-180 µm		47.50	9.60	54.41	20.59	9.58	22.28
90-125 µm		13.67	3.83	13.03	6.57	8.30	5.70
63-90 µm		6.09	4.10	5.24	3.20	7.25	2.13
<63 µm	fines (silt & clay)	6.52	1.83	5.56	14.05	54.10	5.58
	% gravel	0.00%	0.00%	0.00%	0.00%	0.29%	0.00%
	% sand	98.69%	99.55%	99.29%	87.03%	36.70%	94.96%
	% fines	1.30%	0.45%	0.71%	12.97%	63.02%	5.04%

APPENDIX 2 – Results of sediment analyses (Chapter 3)

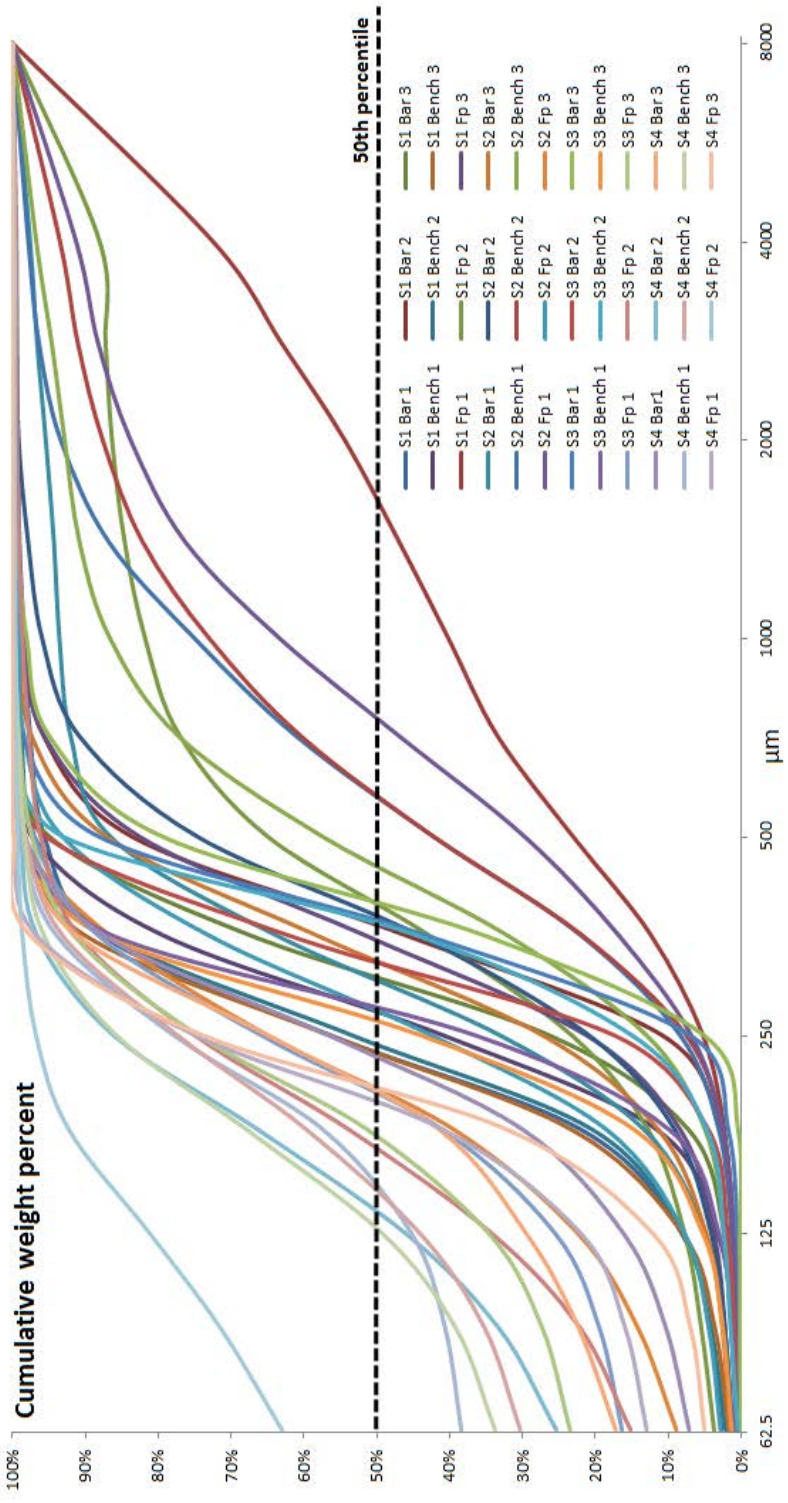
Sediment organic content determined by loss on ignition (LOI)

Site, geomorphic unit & unit replicate	LOI replicate 1	LOI replicate 2	LOI replicate 3	LOI Replicate average
WSF S1bar1	2.079%	2.111%	2.485%	2.225%
WSF S1bar2	3.749%	5.212%	5.760%	4.907%
WSF S1bar3	4.455%	4.481%	4.884%	4.607%
WSF S1ben1	5.726%	3.582%	3.311%	4.206%
WSF S1ben2	5.772%	5.027%	7.429%	6.076%
WSF S1ben3	3.229%	3.381%	3.112%	3.241%
WSF S1fp1	5.270%	5.220%	5.538%	5.343%
WSF S1fp2	6.255%	6.978%	5.355%	6.196%
WSF S1fp3	5.904%	6.519%	5.998%	6.141%
UW S2bar1	2.408%	2.534%	2.356%	2.433%
UW S2bar2	0.793%	0.864%	0.658%	0.771%
UW S2bar3	1.036%	1.017%	0.765%	0.939%
UW S2ben1	2.452%	2.473%	1.843%	2.256%
UW S2ben2	1.414%	1.514%	1.281%	1.403%
UW S2ben3	3.154%	2.854%	2.680%	2.896%
UW S2fp1	7.022%	7.009%	7.603%	7.211%
UW S2fp2	4.292%	3.786%	4.027%	4.035%
UW S2fp3	3.150%	3.367%	3.073%	3.197%
WOW S3bar1	5.052%	7.356%	3.202%	5.203%
WOW S3bar2	2.372%	1.393%	1.175%	1.646%
WOW S3bar3	1.894%	1.828%	1.470%	1.730%
WOW S3ben1	1.352%	1.438%	1.135%	1.308%
WOW S3ben2	3.817%	3.750%	3.867%	3.811%
WOW S3ben3	12.622%	13.723%	18.765%	15.037%
WOW S3fp1	8.761%	9.310%	8.345%	8.805%
WOW S3fp2	7.916%	8.395%	7.685%	7.999%
WOW S3fp3	10.098%	9.664%	9.491%	9.751%
L S4bar1	0.259%	0.437%	0.355%	0.350%
L S4bar2	0.286%	0.319%	0.256%	0.287%
L S4bar3	1.794%	2.451%	1.670%	1.972%
L S4ben1	1.083%	1.280%	0.980%	1.114%
L S4ben2	1.619%	1.674%	1.532%	1.608%
L S4ben3	0.808%	0.872%	0.671%	0.784%
L S4fp1	3.031%	3.481%	3.289%	3.267%
L S4fp2	7.713%	7.891%	7.686%	7.763%
L S4fp3	1.738%	1.517%	1.620%	1.625%

APPENDIX 2 – Results of sediment analyses (Chapter 3)

Calculation of median particle size

Site, geomorphic unit & unit replicate	Median particle size (mm)
WSF S1bar1	2
WSF S1bar2	0.355
WSF S1bar3	0.355
WSF S1ben1	0.355
WSF S1ben2	0.5
WSF S1ben3	0.355
WSF S1fp1	0.25
WSF S1fp2	0.18
WSF S1fp3	0.18
UW S2bar1	0.25
UW S2bar2	0.355
UW S2bar3	0.5
UW S2ben1	0.25
UW S2ben2	0.355
UW S2ben3	0.25
UW S2fp1	0.18
UW S2fp2	0.25
UW S2fp3	0.25
WOW S3bar1	0.5
WOW S3bar2	0.71
WOW S3bar3	0.71
WOW S3ben1	1
WOW S3ben2	0.355
WOW S3ben3	0.25
WOW S3fp1	0.18
WOW S3fp2	0.18
WOW S3fp3	0.18
L S4bar1	0.5
L S4bar2	0.355
L S4bar3	0.5
L S4ben1	0.355
L S4ben2	0.5
L S4ben3	0.355
L S4fp1	0.25
L S4fp2	0.063
L S4fp3	0.25



APPENDIX 3

Species trait data and information sources

APPENDIX 3 - Species trait data and information sources
PART A – Species trait data

Species name	Seedling emergence study 1	Vegetation survey	Seedling emergence study 2	Species Origin	Family	Growth Form *	Longevity ‡	Seed Mass (g/per 1000 seeds)	Seed Length (mm)	Seed Width (mm)	Mode of Seed Dispersal °
Abrophyllum ornans		x		N	Rousseaceae	ST	P	0.049	.	.	A
Acacia parramatensis	x	x		N	Fabaceae	T	P	9.38	3.9	2.1	A
Acacia parvipinnula		x		N	Fabaceae	T	P	11.89	.	.	.
Acacia prominens		x		N	Fabaceae	T	p	15.5	5	.	A
Acacia spp.		x	x	N	Fabaceae	ST	P	9.38	.	.	.
Acetosa sagittata		x		E	Polygonaceae	V	P	1.69	3	1.7	WH
Acetosella vulgaris	x	x	x	E	Polygonaceae	H	P	0.63	1.25	1	WHA
Adiantum aethiopicum	x	x		N	Adiantaceae	F	P	.	.	.	W
Adiantum formosum	x	x	x	N	Adiantaceae	F	P	.	.	.	W
Aira cupaniana		x		E	Poaceae	G	A	0.043	.	.	A
Alternanthera denticulata			x	N	Amaranthaceae	H	A	0.23	1.5	1	A
Anagallis arvensis	x	x	x	E	Primulaceae	H	P	0.4782	1.25	0.855	H
Angophora costata		x		N	Myrtaceae	T	P	16.1	4	4	WH
Aphanopetalum resinosum		x		N	Aphanopetalaceae	V	P	.	2.5	.	W
Araujia sericifera		x		E	Apocynaceae	V	P	9.62	6.5	2.4	WH
Aristida spp.			x		Poaceae			.	.	.	.
Austrocynoglossum latifolium	x			N	Boraginaceae	H	P	.	2.5-3.5	1.5-2	A
Axonopus fissifolius	x	x	x	E	Poaceae	SR	P	0.371	.	.	WU
Backhousia myrtifolia		x		N	Myrtaceae	ST	P	.	1.25	1	U?
Bacopa monnieri	x			N	Scrophulariaceae	H	P	.	0.6	0.35	H
Bidens pilosa			x	E	Asteraceae	H	A	2.1	12	1	AWH
Blechnum cartilagineum		x		N	Blechnaceae	F	P	.	.	.	W
Breynia oblongifolia		x		N	Euphorbiaceae	S	P	5.66	3.25	.	A
Briza minor	x	x	x	E	Poaceae	G	A	0.318	2.2	.	WH
Bromus catharticus		x		E	Poaceae	G	P	7.7	9	2	WA
Callicoma serratifolia	x		x	N	Cunoniaceae	ST	P	.	1.2	0.7	W
Calochlaena dubia	x	x	x	N	Dicksoniaceae	F	P	NA	.	.	.
Carex inversa	x		x	N	Cyperaceae	SR	P	0.37	.	.	WH
Carex maculata	x		x	N	Cyperaceae	SR	P	.	.	.	H
Cayratia clematidea		x		N	Vitaceae	V	P	21.288	4	4	A
Centaurium tenuiflorum	x			E	Gentianaceae	H	A	0.014	.	.	W
Centella asiatica	x	x	x	N	Apiaceae	H	P	1.501	3.5	2	H
Centipeda minima	x		x	N	Asteraceae	H	A	0.02	1	0.4	H
Centrolepis fascicularis			x	N	Centrolepidaceae	SR	P	0.13	0.5	0.35	H
Cerastium glomeratum	x	x	x	E	Caryophyllaceae	H	A	0.048	0.4	0.6	WU
Ceratopetalum apetalum		x		N	Cunoniaceae	T	P	24.39	3	.	.
Cestrum parqui		x		E	Solanaceae	S	P	4.5	3	2	AW
Cheilanthes sieberi subsp. sieberi	x		x	N	Adiantaceae	F	P	NA	.	.	.
Cineraria lyratiformis	x			E	Asteraceae	H	A	0.46	.	.	W
Cirsium vulgare		x	x	E	Asteraceae	H	B	2.9	4	1.5	WH

APPENDIX 3 - Species trait data and information sources
PART A – Species trait data

Species name	Seedling emergence study 1	Vegetation survey	Seedling emergence study 2	Species Origin	Family	Growth Form *	Longevity ‡	Seed Mass (g/per 1000 seeds)	Seed Length (mm)	Seed Width (mm)	Mode of Seed Dispersal °
Cissus hypoglauca	x			N	Vitaceae	V	P	39.11	6.5	4.5	A
Clematis aristata	x	x		N	Ranunculaceae	V	P	0.29	2.5	1	W
Clerodendrum tomentosum		x		N	Verbenaceae	ST		77.922	10	6	A
Commelina cyanea	x	x	x	N	Commelinaceae	H	P	6.0225	2.5	1.5	U
Conyza bonariensis		x		E	Asteraceae	H	A	0.1	1.5	.	W
Conyza canadensis			x	E	Asteraceae	H	A	0.07	1	0.2	W
Conyza parva	x	x	x	E	Asteraceae	H	A	0.05	.	.	W
Conyza sumatrensis	x	x	x	E	Asteraceae	H	A	0.04	1.26	1.09	W
Cotula australis	x	x		N	Asteraceae	H	P	0.0526	1.25	1	W
Cryptocarya microneura		x		N	Lauraceae	ST	P	.	17	9.5	A
Cynodon dactylon	x	x	x	N	Poaceae	G	P	0.2491	2.5	1	WUH
Cyperus aggregatus	x			E	Cyperaceae	SR	P	.	1.7	0.9	WH
Cyperus brevifolius	x		x	E	Cyperaceae	SR	P	.	1-1.5	0.5-0.7	WH
Cyperus congestus			x	E	Cyperaceae	SR	P	0.24	1.5	0.6	WH
Cyperus difformis	x			N	Cyperaceae	SR	A	0.06	0.6	0.3	WH
Cyperus enervis		x		N	Cyperaceae	SR	P	.	1.25	0.8	WH
Cyperus eragrostis	x		x	E	Cyperaceae	SR	P	0.1297	1.4	0.5	HA
Cyperus flavescens	x		x	N	Cyperaceae	SR	A	0.07	1	0.7	WH
Cyperus flavidus	x			N	Cyperaceae	SR	P	0.19	1	0.5	WH
Cyperus gracilis	x		x	N	Cyperaceae	SR	P	.	1.2	0.8	WH
Cyperus imbecillis		x	x		Cyperaceae	SR	P	0.12	0.9	0.75	WH
Cyperus laevis	x		x	N	Cyperaceae	SR	P	.	1	0.8	WH
Cyperus lucidus			x		Cyperaceae	SR	.	.	2.7	0.7	WH
Cyperus polystachyos	x		x	N	Cyperaceae	SR	P	0.06	1	0.4	WH
Cyperus sanguinolentus	x		x	N	Cyperaceae	SR	P	0.135	1.1	0.9	WH
Cyperus sesquiflorus	x		x	E	Cyperaceae	SR	P	0.14	1.15	0.9	WH
Cyperus spp.		x			Cyperaceae	SR	.	.	.	.	WH
Cyperus tetraphyllus	x			N	Cyperaceae	SR	P	.	1.15	0.8	WH
Cyperus trinervis	x		x	N	Cyperaceae	SR	P	0.12	1	0.6	WH
Daphnandra apatela		x		N	Monimiaceae	T	P	4	5	.	W
Daucus glochidiatus	x	x	x	N	Apiaceae	H	A	2.18	4	3	A
Davallia solida var. pyxidata	x	x		N	Davalliaceae	F	P	NA	F	F	.
Delairea odorata		x		E	Asteraceae	V	P	0.3	2	0.5	WH
Desmodium varians		x		N	Fabaceae	H	P	.	3	1.9	A
Dichondra repens	x	x		N	Convolvulaceae	H	P	3.2	1.4	1.2	H
Digitaria ciliaris	x		x	E	Poaceae	G	A	0.556	2.3	1	AW
Digitaria didactyla		x		E	Poaceae	G	A	0.556	2.3	1	AW
Diospyros australis		x		N	Ebenaceae	ST	P	217	11.75	6	A
Dodonaea triquetra		x		N	Sapindaceae	S	P	3.4058	2.6	2.2	W
Doodia aspera	x	x		N	Blechnaceae	F	P	.	.	.	.
Doodia caudata	x			N	Blechnaceae	SR	P	.	.	.	W

APPENDIX 3 - Species trait data and information sources
PART A – Species trait data

Species name	Seedling emergence study 1	Vegetation survey	Seedling emergence study 2	Species Origin	Family	Growth Form *	Longevity ‡	Seed Mass (g/per 1000 seeds)	Seed Length (mm)	Seed Width (mm)	Mode of Seed Dispersal °
Doryphora sassafras		x		N	Monimiaceae	T	P		11.000		
Dysoxylum fraserianum		x		N	Meliaceae	T	P	171.95	.	.	A
Echinopogon ovatus	x			N	Poaceae	G	P	.	.	.	A
Ehrharta calycina		x		E	Poaceae	G	P	0.7	.	.	AW
Ehrharta erecta	x	x	x	E	Poaceae	G	P	2.58	3.5	1.7	AW
Einadia hastata	x	x	x	N	Chenopodiaceae	S	P	0.496	1.5	.	A
Elatine gratioloides	x			N	Elatinaceae	A	P	0.05	0.6	2	H
Eleocharis sphacelata		x		N	Cyperaceae	SR	P	3.34	2	.	HW
Entolasia marginata	x	x		N	Poaceae	G	P	.	.	.	.
Entolasia stricta	x	x	x	N	Poaceae	G	P	1.4525	.	.	.
Eragrostis brownii			x	N	Poaceae	G	P	0.07	0.5-0.8	0.3-0.5	.
Eucalyptus saligna		x		N	Myrtaceae	T	P	0.7867	1	0.3	W
Eucalyptus spp	x		x	N	Myrtaceae	T	P	.	.	.	.
Eucalytpus amplifolia	x			N	Myrtaceae	T	P	2.55	1.5	0.5	U
Euchiton sphaericus	x			N	Asteraceae	H	A	0.0325	0.7	.	W
Euchiton japonicus	x			N	Asteraceae	H	P	0.03	0.7	.	U
Facilis retusa		x	x	E	Asteraceae	H	P	0.35	1.25	.	W
Ficus coronata	x	x	x	N	Moraceae	ST	P	0.39	.	.	A
Ficus spp.		x			Moraceae	ST		.	.	.	
Fimbristylis dichotoma	x			N	Cyperaceae	SR	P	0.1996	1	0.8	U
Gahnia aspera		x		N	Cyperaceae	SR	P	28.75	4.5	3	A
Galium binifolium		x		N	Rubiaceae	H	P	1.34	.	.	A
Gamochaeta americana	x	x	x	E	Asteraceae	H	B	0.006	0.5	.	W
Gamochaeta calviceps	x	x	x	E	Asteraceae	H	A	.	0.5	.	W
Gamochaeta pensylvanica		x		E	Asteraceae	H	A	.	0.4	.	W
Gamochaeta purpurea		x		E	Asteraceae	H	B	0.037	0.5	.	W
Geitonoplesium cymosum		x		N	Luzuriagaceae	V	P	20.49	5	3	A
Geranium homeanum	x	x	x	N	Geraniaceae	H	P	2.5	2	1.2	E
Glochidion fernandii		x		N	Euphorbiaceae	ST	P	2.02	4.5	4.375	A
Glycine microphylla		x		N	Fabaceae	H	P	.	.	.	U
Gratiola peruviana	x		x	N	Scrophulariaceae	H	P	0.02	.	.	H
Guioa semiglauca		x		N	Sapindaceae	T	P	41	.	.	A
Hibbertia scandens		x		N	Dilleniaceae	V	P	7.25	3.3	2.5	A
Homalanthus populifolius	x			N	Euphorbiaceae	ST	P	.	.	.	A
Hydrocotyle bonariensis		x		N	Apiaceae	H	P	1.3	.	.	.
Hydrocotyle peduncularis	x	x	x	N	Apiaceae	H	P	0.4438	.	.	.
Hydrocotyle tripartita	x	x	x	N	Apiaceae	H	P	0.33	.	0.5	.
Hypericum gramineum	x	x	x	N	Clusiaceae	H	P	0.019	0.4	0.25	WU
Hypericum japonicum	x		x	N	Clusiaceae	H	A	.	.	.	W
Hypericum perforatum			x	E	Clusiaceae	S	P	0.14	1	0.5	AWH
Hypochoeris radicata	x	x	x	E	Asteraceae	H	P	0.8284	7	0.75	W

APPENDIX 3 - Species trait data and information sources
PART A – Species trait data

Species name	Seedling emergence study 1	Vegetation survey	Seedling emergence study 2	Species Origin	Family	Growth Form *	Longevity ‡	Seed Mass (g/per 1000 seeds)	Seed Length (mm)	Seed Width (mm)	Mode of Seed Dispersal °
Hypolepis meulleri		x		N		.	.	.	.	.	.
Imperata cylindrica		x		N	Poaceae	G	P	0.114	1.40	0.50	WA
Isachne globosa		x		N	Poaceae	AG	P	0.8	1.2	1	H
Isolepis inundata	x	x	x	N	Cyperaceae	SR	P	0.065	0.85	0.7	H
Isolepis prolifer	x	x	x	E	Cyperaceae	SR	P	0.04	1	0.4	H
Juncus articulatus	x	x		E	Juncaceae	SR	P	0.04	0.7	0.33	H
Juncus bufonius	x	x	x	N	Juncaceae	SR	A	0.0172	0.6	0.35	H
Juncus capillaceus	x	x	x	E	Juncaceae	SR	P	0.02	0.6	0.4	H
Juncus cognatus	x	x	x	E	Juncaceae	SR	P	.	.	.	H
Juncus continuus	x	x	x	N	Juncaceae	SR	P	.	0.5	0.3	H
Juncus effusus		x		E	Juncaceae	SR	P	0.02	0.52	0.24	H
Juncus fockei	x			N	Juncaceae	SR	P	0.01	0.5-0.6	0.2-0.3	H
Juncus homalocaulis	x			N	Juncaceae	SR		0.03	.	.	H
Juncus microcephalus	x			E	Juncaceae	SR	P	.	0.4-0.5	0.2	H
Juncus planifolius	x	x	x	N	Juncaceae	SR	P	0.0133	0.45	0.3	H
Juncus prismatocarpus	x		x	N	Juncaceae	SR	P	0.01	0.3	0.2	W
Juncus remotiflorus			x	N	Juncaceae	SR	P	.	.	.	H
Juncus spp.	x			.	Juncaceae	SR	.	.	.	.	H
Juncus usitatus	x			N	Juncaceae	SR	P	0.01	0.4	0.2	H
Lantana camara		x		E	Verbenaceae	S	P	16	4	2.5	A
Lepidosperma limicola	x		x	N	Cyperaceae	SR	P	5.36	3	1.25	A
Lobelia anceps	x			N	Lobeliaceae	H	P	0.01	0.4167	0.2708	W
Lomandra longifolia	x	x	x	N	Lomandraceae	H	P	9.045	3.4	2.3	S
Lomatia myricoides		x		N	Proteaceae	ST	P	6.45	.	.	W
Lonicera japonica				E	Caprifoliaceae	V	P	1.8	2.5	2	HA
Marsdenia rostrata		x		N	Apocynaceae	SV	P	23.598	8.6	5	WU
Marsdenia suaveolens		x		N	Apocynaceae	SV	P	22.59	8.55	4.55	WU
Microlaena stipoides	x	x	x	N	Poaceae	G	P	4.97	10	2	AU
Modiola caroliniana				E	Malvaceae	H	P	0.7	1.4	1.2	U?
Morinda jasminoides	x	x		N	Rubiaceae	V	P	7.86	3.1	1.7	A
Neolitsea dealbata		x		N	Lauraceae	ST	P	146.02	6.25	6.25	A
Oenothera spp.	x	x		E	Onagraceae	H	P	0.4286	.	.	.
Oplismenus aemulus	x	x	x	N	Poaceae	G	P	0.89	.	.	W
Oplismenus imbeccilus	x			N	Poaceae	G	P	0.915	.	.	UA
Oxalis debilis var. corymbosa		x		E	Oxalidaceae	H	P	.	.	.	B
Oxalis perennans	x	x	x	N	Oxalidaceae	H	P	0.6378	1.2	1	B
Ozothamnus diosmifolius	x			N	Asteraceae	S	P	0.1125	0.75	0.4	W
Pandorea pandorana		x		N	Bignoniaceae	V	P	3.8	8	7	WU
Paronychia brasiliana		x		E	Caryophyllaceae	H	P	0.215	1	.	W
Passiflora edulis		x		E	Passifloraceae	V	P	15.46	5	4	A
Pellaea falcata		x		N	Adiantaceae	F	P	.	.	.	.
Pennisetum clandestinum		x		E	Poaceae	G	P	2.18	2.325	1.1	WA

APPENDIX 3 - Species trait data and information sources
PART A – Species trait data

Species name	Seedling emergence study 1	Vegetation survey	Seedling emergence study 2	Species Origin	Family	Growth Form *	Longevity ‡	Seed Mass (g/per 1000 seeds)	Seed Length (mm)	Seed Width (mm)	Mode of Seed Dispersal °
Persicaria decipiens	x			N	Polygonaceae	H	P	1.07	1.75	1.5	WH
Persicaria lapathifolia	x	x	x	N	Polygonaceae	H	B	1.43	1.75	1.45	WH
Persicaria prostrata		x		N	Polygonaceae	H	P	1.2	1.75	1.25	WH
Persicaria strigosa	x	x		N	Polygonaceae	H	P	3.287	2.65	2	WH
Petrorhagia dubia		x		E	Caryophyllaceae	H	A	0.265	1.3	0.9	.
Philydrum lanuginosum	x		x	N	Philydraceae	H	P	0.04	0.85	0.35	WH
Phytolacca octandra	x			E	Phytolaccaceae	H	P	4.7875	2	.	A
Plantago lanceolata	x	x	x	E	Plantaginaceae	H	P	1.3	2.7	1.25	AW
Plectranthus parviflorus		x	x	N	Lamiaceae	S	P	0.42	1.2	1	U
Poa annua	x	x	x	E	Poaceae	G	A	0.214	2.6	0.85	AWH
Polycarpon tetraphyllum		x	x	E	Caryophyllaceae	H	A	0.05	1.5	0.5	U
Polypogon littoralis			x		Poaceae	G	.	.	.	.	.
Pratia purpurascens	x	x	x	N	Lobeliaceae	H	P	0.2	.	.	U
Prostanthera ovalifolia		x		N	Lamiaceae	S	P	1.55	.	.	.
Pseuderanthemum variabile	x	x		N	Acanthaceae	H	P	.	.	.	.
Pteridium esculentum		x		N	Dennstaedtiaceae	F	P	F	F	F	.
Pteris tremula	x			N	Pteridaceae	F	.	NA	.	.	.
Ranunculus plebeius		x		N	Ranunculaceae	H	P	.	2.3	1.6	UH
Rhodomyrtus psidioides		x		N	Myrtaceae	T	P	1.49	.	3	A
Romulaea rosea		x		E	Iridaceae	H	P	3.52	1.75	1.5	A
Rubus parvifolius	x	x	x	N	Rosaceae	S	P	0.9755	2	.	A
Rubus rosifolius	x	x	x	N	Rosaceae	S	P	0.6	1.8	1	A
Rubus spp.		x		.	Rosaceae	.	.	.	.	.	.
Rubus moluccanus var. trilobus	x	x		N	Rosaceae	S	P	0.85	2.8	1.3	A
Rumex conglomeratus		x		E	Polygonaceae	H	P	1.5	1.5	1	A
Rumex crispus		x		E	Polygonaceae	H	P	1.5	1.8	1.2	AW
Sarcopetalum harveyanum		x		N	Rutaceae	ST	P	13	6	4.5	A
Senecio madagascariansis	x	x	x	E	Asteraceae	H	A B	0.26	2	0.25	W
Senecio minimus	x			N	Asteraceae	H	A	0.15	2	.	W
Setaria parviflora	x	x		E	Poaceae	G	P	1.53	2	1.2	WA
Sida rhombifolia	x	x	x	E	Malvaceae	S	P	2.59	2.8	2	AH
Sigesbeckia orientalis	x	x	x	N	Asteraceae	H	A	1.27	2.5	2.59	WA
Sisyrinchium iridifolium			x	E	Iridaceae	H	A	.	.	.	.
Sisyrinchium spp. A	x		x	E	Iridaceae	H	A	0.57	0.6	0.6	.
Smilax australis		x		N	Smilacaceae	V	P	40.76	4.5	4	A
Solanum americanum	x	x	x	N	Solanaceae	H	B	0.59	2	1.7	A
Solanum aviculare	x			N	Solanaceae	S	P	0.8	.	.	.
Solanum nigrum	x	x	x	E	Solanaceae	H	A	0.775	2	1.5	A
Solanum linnaeanum	x		x	N	Solanaceae	S	P	4.86	.	.	A
Soliva sessilis	x	x		E	Asteraceae	H	A	0.942	5	3	A
Sonchus asper		x		E	Asteraceae	H	A	0.28	2.5	1	W

APPENDIX 3 - Species trait data and information sources
PART A – Species trait data

Species name	Seedling emergence study 1	Vegetation survey	Seedling emergence study 2	Species Origin †	Family	Growth Form *	Longevity ‡	Seed Mass (g/per 1000 seeds)	Seed Length (mm)	Seed Width (mm)	Mode of Seed Dispersal °
Sparganium subglobosum		x		N	Sparganiaceae	A	P	.	.	.	H
Stellaria flaccida		x	x	N	Caryophyllaceae	H	P	0.422	0.45	0.35	U
Stellaria media	x	x	x	E	Caryophyllaceae	H	A	0.4	1.1	1.1	U
Stephania japonica		x		N	Menispermaceae	V	P	19.72	4.75	4.75	A
Syzygium australe		x		N	Myrtaceae	T	P	259	12	10	A
Tagetes minuta			x	E	Asteraceae	H	A	1.18	7	0.8	A
Tradescantia fluminensis	x	x	x	E	Commelinaceae	H	P	3.01	.	.	U
Trema tomentosa	x	x		N	Ulmaceae	ST	P	4.86	2.25	2	A
Trifolium arvense	x	x		E	Fabaceae	H	A	0.4	0.9	0.7	W
Trifolium dubium		x	x	E	Fabaceae	H	A	0.4	1	0.8	.
Trifolium repens	x	x	x	E	Fabaceae	H	P	0.63	1.2	1	.
Tristaniopsis laurina		x		N	Myrtaceae	T	P	1.6	4	1.5	W
Urtica incisa		x		N	Uriticaceae	H	P	0.24	2	1.5	U
Uritca urens		x		E	Uriticaceae	H	A	0.5195	2.12	1.5	U
Verbena bonariensis	x	x	x	E	Verbenaceae	H	P	0.17	1	0.3	WH
Veronica persica	x	x		E	Plantaginaceae	H	?	0.759	1.7	1.3	.
Veronica plebeia	x	x	x	N	Plantaginaceae	H	P	.	1	0.6	.
Viola hederacea	x	x		N	Violaceae	H	P	0.88	1.5	0.9	.
Vulpia muralis		x	x	E	Poaceae	G	A	0.1	.	.	.
Vulpia myuros	x	x		E	Poaceae	G	A	0.48	5	0.5	A
Wahlenbergia communis	x	x		N	Campanulaceae	H	P	0.04	0.5	0.2	W
Wahlenbergia gracilis	x	x	x	N	Campanulaceae	H	P	0.0668	0.3	0.2	W
Xanthorrhoea spp		x		N	Xanthorrhoeaceae	H	P	20.774	.	.	U

Species trait data key to abbreviations

† Species origin	**N**	Native
	E	Exotic
* Growth form	**A**	Aquatic
	F	Fern
	G	Grass
	H	Herb
	S	Shrub
	SR	Sedge/Rush
	S	Shrub
	ST	Shrub/Tree
	T	Tree
	V	Vine
‡ Longevity	**A**	Annual
	B	Biennial
	P	Perennial
° Seed dispersal mechanism	**A**	Animal (including invertebrates, mammals, birds)
	B	Ballistic
	H	Hydrochory (water-mediated)
	W	Wind
	U	Unassisted

APPENDIX 3 – Species trait data with information sources

PART C - Internet resources and databases

Abbreviations indicate internet resources and databases with explanation of abbreviations provided in Part C. References for published data citations provided in Part D.

Abrophyllum ornans
KEW; PlantNET; Benson and McDougall 1993

Acacia parramatensis
FloraBase; KEW; PlantNET

Acacia parvipinnula
FloraBase; KEW; PlantNET

Acacia prominens
FloraBase; KEW; NSWOEH; PlantNET; WWWattle

Acacia spp.
FloraBase; KEW; PlantNET

Acetosa sagittata
FloraBase; KEW; PlantNET; UQLD

Acetosella vulgaris
FloraBase; KEW; PlantNET; UQLD

Adiantum aethiopicum
FloraBase; KEW; PlantNET

Adiantum formosum
FloraBase; KEW; PlantNET

Aira cupaniana
FloraBase; KEW; PlantNET; Crossman et al 2011

Alternanthera denticulata
FloraBase; KEW; PlantNET; TasDPIPWE

Anagallis arvensis
FloraBase; KEW; PlantNET; UQLD

Angophora costata
FloraBase; KEW; PlantNET

Aphanopetalum resinosum
FloraBase; KEW; PlantNET

Araujia sericifera
FloraBase; Google images; KEW; PlantNET; UQLD; Vivian-Smith and Panetta 1995,

Austrocynoglossum cymosum
FloraBase; KEW; PlantNET; TasDPIPWE

Austrocynoglossum latifolium
FloraBase; KEW; PlantNET; Mill 1989

Axonopus fissifolius
CSIROtrop; FloraBase; KEW; PlantNET

Backhousia myrtifolia
FloraBase; KEW; PlantNET; Harrington et al 2012

Bacopa monnieri
FloraBase; KEW; PlantNET

Bidens pilosa
FloraBase; KEW; PlantNET; Navie and Sheldon 2008

Blechnum cartilagineum
FloraBase; KEW; PlantNET; TasDPIPWE; Robinson 1991

Breynia oblongifolia
FloraBase; KEW; PlantNET

APPENDIX 3 – Species trait data with information sources
PART C - Internet resources and databases

Briza minor
FloraBase; KEW; PlantNET; UQLD

Bromus catharticus
FloraBase; Google images; KEW; PlantNET; UQLD;

Callicoma serratifolia
FloraBase; Google images; PlantNET; Kennedy and Prakash 1981; Royer et al 2009

Calochlaena dubia
FloraBase; KEW; PlantNET

Carex inversa
FloraBase; KEW; PlantNET

Carex maculata
FloraBase; PlantNET

Cayratia clematidea
FloraBase; KEW; PlantNET

Centaurium tenuiflorum
FloraBase; KEW; PlantNET

Centella asiatica
FloraBase; KEW; PlantNET; Singh and Singh 2002

Centipeda minima
FloraBase; KEW; PlantNET; Walsh 2001

Centrolepis fascicularis
FloraBase; KEW; PlantNET; Cooke 1991

Cerastium glomeratum
FloraBase; KEW; PlantNET

Ceratopetalum apetalum
FloraBase; KEW; PlantNET; Benson and McDougall 1993; Herwitz 1991

Cestrum parqui
FloraBase; KEW; PlantNET; WeedWise; Griffiths 2004

Cheilanthes sieberi subsp. sieberi
FloraBase; KEW; PlantNET

Cineraria lyratiformis
KEW (seed mass average genus average); PlantNET

Cirsium vulgare
FloraBase; KEW; PlantNET

Cissus hypoglauca
FloraBase; KEW; PlantNET

Clematis aristata
FloraBase; KEW; PlantNET

Clerodendrum tomentosum
FloraBase; KEW; PlantNET; Langkamp and Plaisted 1987

Commelina cyanea
FloraBase; KEW; PlantNET

Conyza bonariensis
FloraBase; KEW; PlantNET; Funes et al 1999

Conyza canadensis
FloraBase; KEW; PlantNET; Google images

Conyza parva
FloraBase; KEW; PlantNET; Funes et al 1999

Conyza sumatrensis

FloraBase; KEW; PlantNET; Funes et al 1999

Cotula australis

FloraBase; KEW; PlantNET

Cryptocarya microneura

FloraBase; KEW; PlantNET

Cynodon dactylon

ATRP; FloraBase; KEW; PlantNET; Google images

Cyperus aggregatus

FloraBase; PlantNET

Cyperus brevifolius

PlantNET

Cyperus congestus

KEW; PlantNET (seed dimensions from image)

Cyperus difformis

KEW; PlantNET

Cyperus enervis

KEW; PlantNET

Cyperus eragrostis

KEW; PlantNET (seed dimensions); FloraBase

Cyperus flavescens

PlantNET

Cyperus flavidus

FloraBase; PlantNET

Cyperus gracilis

FloraBase; KEW; PlantNET

Cyperus imbecillis

PlantNET

Cyperus laevis

KEW; PlantNET; FloraBase

Cyperus lucidus

PlantNET

Cyperus polystachyos

FloraBase; PlantNET

Cyperus sanguinolentus

FloraBase; PlantNET

Cyperus sesquiflorus

FloraBase; PlantNET

Cyperus tetraphyllus

FloraBase; KEW; PlantNET

Cyperus trinervis

FloraBase; KEW; PlantNET

Daphnandra apatela

FloraBase; KEW; PlantNET; ABRS

Daucus glochidiatus

FloraBase; KEW; PlantNET; Sweedman and Merritt 2006

Davallia solida var. pyxidata

PlantNET

Delairea odorata

FloraBase; GISD; PlantNET; Robinson date? (seed width derived from photos within and based on length provided by PlantNET

Desmodium varians

FloraBase; KEW; PlantNET; TasDPIPWE

Dichondra repens

FloraBase; KEW; PlantNET

Digitaria ciliaris

FloraBase; KEW; PlantNET; Google images

Digitaria didactyla

FloraBase; KEW; PlantNET; Google images

Diospyros australis

FloraBase; KEW; PlantNET

Dodonaea triquetra

ATRP; FloraBase; KEW; PlantNET

Doodia aspera

FloraBase; KEW; PlantNET

Doodia caudata

FloraBase; KEW; PlantNET

Doryphora sassafras

FloraBase; KEW; PlantNET

Dysoxylum fraserianum

FloraBase; KEW; PlantNET; Boland et al 2006 CHECK

Echinopogon ovatus

FloraBase; KEW; PlantNET

Ehrharta calycina

FloraBase; KEW; PlantNET;

Ehrharta erecta

FloraBase; KEW; PlantNET; SydWeeds; Google images

Einadia hastata

FloraBase; KEW; PlantNET

Elatine gratioloides

FloraBase; KEW; PlantNET (seed dimensions)

Eleocharis sphacelata

FloraBase; KEW; PlantNET

Entolasia marginata

PlantNET

Entolasia stricta

FloraBase; KEW; PlantNET

Eragrostis brownii

FloraBase; KEW; PlantNET

Eucalyptus saligna

FloraBase; KEW; PlantNET

Eucalytpus amplifolia

FloraBase; KEW; PlantNET

Euchiton sphaericus

FloraBase; KEW; PlantNET

Euchiton japonicus

FloraBase; KEW; PlantNET

Facilis retusa

KEW; PlantNET; Funes et al 1999; Thompson et al 1997

Ficus coronata

FloraBase; KEW; PlantNET

Fimbristylis dichotoma

ATRP; FloraBase; KEW; PlantNET

Gahnia aspera

FloraBase; KEW; PlantNET

Galium binifolium

FloraBase; KEW; PlantNET

Gamochaeta americana

FloraBase; KEW; PlantNET; Funes et al 1999

Gamochaeta calviceps

FloraBase; PlantNET; Funes et al 1999

Gamochaeta pensylvanica

FloraBase; PlantNET

Gamochaeta purpurea

KEW; PlantNET; Funes et al 1999

Geitonoplesium cymosum

ATRP; KEW; PlantNET;

Geranium homeanum

FloraBase; KEW; PlantNET

Glochidion fernandii var.

KEW; PlantNET; FloraBase

Glycine microphylla

PlantNET; TasDPIPWE; Sweedman and Merritt 2006

Gratiola peruviana

FloraBase; KEW; PlantNET

Guioa semiglauca

FloraBase; KEW; PlantNET

Hibbertia scandens

FloraBase; KEW; PlantNET

Homalanthus populifolius

PlantNET; Grubb and Metcalfe 1996

Hydrocotyle bonariensis

FloraBase; KEW; PlantNET

Hydrocotyle peduncularis

KEW; PlantNET

Hydrocotyle tripartita

KEW; PlantNET; Webb and Johnson 1982

Hypericum gramineum

KEW; PlantNET; Google images; Jurade et al 1991; McIntyre et al 2005

Hypericum japonicum

KEW; PlantNET; McIntyre et al 2005

Hypericum perforatum

KEW; PlantNET; Groves et al 1995

Hypochoeris radicata

PlantNet; Miles 1974; McIntyre et al 1995; Pérez-Fernández et al. 2000; Edwards et al 2001; Pico et al 2004

Hypolepis meulleri

PlantNET

Imperata cylindrica

KEW; PlantNET; Ridley 1930; Odgers and Rogers 1993; Scher and Walters 2010

Isachne globosa

KEW; PlantNET; WSSA

Isolepis inundata

FloraBase; KEW; PlantNET; Moles et al 2000

Isolepis prolifer

FloraBase; KEW; PlantNET; Bell 1993; Moles et al 2000

Juncus articulatus

FloraBase; KEW; PlantNET; Grime 1981

Juncus articulatus

KEW; PlantNET; FloraBase; Grime 1981

Juncus bufonius

KEW; PlantNET; Grime 1981; McIntyre et al 1995; Peco et al 2003; Stevens 1932;

Juncus capillaceus

KEW; PlantNET; Balslev, 1996; Peco et al 2003; Thompson et al 1997

Juncus cognatus

PlantNET; FloraBase

Juncus continuus

PlantNET; FloraBase

Juncus effusus

KEW; PlantNET; FloraBase; Ervin and Wetzel 2001

Juncus fockei

KEW; PlantNET; Kirschner and Australian Biological Resources Study 2002

Juncus homalocaulis

KEW; PlantNET

Juncus microcephalus

FloraBase; PlantNETKirschner and Australian Biological Resources Study 2002

Juncus planifolius

KEW; PlantNET; Balslev 1996; Moles et al 2000

Juncus prismatocarpus

KEW; PlantNET; FloraBase

Juncus remotiflorus

PlantNET

Juncus usitatus

Florabase; KEW; PlantNET

Lantana camara

AustWC; Florabase; KEW; PlantNET; Google images

Lepidosperma limicola

Florabase; KEW; PlantNET

Lobelia anceps

Florabase; KEW; PlantNET

Lomandra longifolia

Florabase; KEW; PlantNET

Lomatia myricoides

Florabase; KEW; PlantNET

Lonicera japonica

AustWC; Florabase; KEW; PlantNET; Google images; Schierenbeck 2004

Marsdenia rostrata
ATRP; KEW (genus average for seed mass)

Marsdenia suaveolens
Florabase; KEW; PlantNET

Microlaena stipoides
KEW; PlantNET; Google images

Modiola caroliniana
KEW; PaDIL; PlantNET

Morinda jasminoides
KEW; PlantNET; Grubb et al. 1998

Neolitsea dealbata
ATRP; Florabase; KEW; PlantNET

Oenothera spp.
FloraBase; KEW (genus seed mass average); PlantNET

Oplismenus aemulus
Florabase; KEW; PlantNET

Oplismenus imbeccilus
Florabase; KEW; PlantNET

Oxalis debilis var. corymbosa
Florabase; KEW; PlantNET

Oxalis perennans
Florabase; KEW; PlantNET; Mazer 1989; Thompson et al 1997

Ozothamnus diosmifolius
Florabase; KEW; PlantNET; Moles et al 2003

Pandorea pandorana
Florabase; KEW; PlantNET; Sweedman and Merritt 2006

Paronychia brasiliana
Florabase; KEW; PlantNET; McIntyre et al 1995

Passiflora edulis
ATRP; Florabase; KEW; PlantNET; Felfoldi 1980; Navie and Adkins 2008

Pellaea falcata
Florabase; KEW; PlantNET

Pennisetum clandestinum
FloraBase; KEW; PlantNET; Felfoldi 1980

Persicaria decipiens
Florabase; KEW; PlantNET

Persicaria lapathifolia
Florabase; KEW; PlantNET; Thompson et al 1997

Persicaria prostrata
Florabase; KEW; PlantNET

Persicaria strigosa
Florabase; KEW; PlantNET

Petrorhagia dubia
Florabase; KEW; PaDIL; PlantNET

Philydrum lanuginosum
ATRP; Florabase; KEW; PlantNET

Phytolacca octandra
ATRP; Florabase; KEW; PlantNET

Plantago lanceolata

ATRP; Florabase; KEW; PlantNET

Plectranthus parviflorus

ATRP; Florabase; KEW; PlantNET

Poa annua

Florabase; KEW; PlantNET; Grime 1981; Milberg et al 2000

Polycarpon tetraphyllum

Florabase; HerbiGuide; KEW; PlantNET; Kool et al 2007

Polypogon littoralis

Florabase; KEW; PlantNET

Pratia purpurascens

KEW; PlantNET; Funes et al 1999

Prostanthera ovalifolia

Florabase; KEW; PlantNET

Pseuderanthemum variabile

ATRP; FloraBase; PlantNET

Pteridium esculentum

Florabase; KEW; PlantNET

Pteris tremula

KEW; PlantNET

Ranunculus plebeius

PlantNET (seed dimensions from description and photo); Thompson et al 1997

Rhodomyrtus psidioides

KEW; PlantNET; Scott 1978

Romulaea rosea

Florabase; KEW; PlantNET; Eddy and Smith 1975

Rubus parvifolius

Florabase; KEW; PlantNET; Hummer and Peacock 1994; Howel et al 1995; Oleskevic 1996

Rubus rosifolius

Florabase; KEW; PlantNET; Google images

Rubus spp.

PlantNET

Rubus moluccanus var. trilobus

Florabase; KEW; PlantNET; Google images

Rumex conglomeratus

Florabase; KEW; PlantNET; Google images

Rumex crispus

Florabase; KEW; PlantNET; Google images; Earle and Jones 1962; Grime et al 1981; Rozefelds 1991

Sarcopetalum harveyanum

ATRP; Florabase; KEW; PlantNET; Hartley 1982; Grubb et al 1998

Senecio madagascariansis

AustWC; Florabase; KEW; PlantNET; Google images; Sindel 1996

Senecio minimus

Florabase; KEW; PlantNET

Setaria parviflora

Florabase; KEW; PlantNET; Google images

Sida rhombifolia

Florabase; KEW; PlantNET

Sigesbeckia orientalis

Florabase; KEW; PlantNET; Van der Pijl 1982

Sisyrinchium iridifolium

Florabase; KEW; PlantNET

Sisyrinchium spp. A

ATRP; Florabase; KEW; PlantNET

Smilax australis

ATRP; Florabase; KEW; PlantNET

Solanum americanum

Florabase; KEW; PlantNET; UQLD; Google images

Solanum aviculare

Florabase; KEW; PlantNET

Solanum nigrum

Florabase; KEW; PlantNET; Google images

Solanum linnaeanum

Florabase; KEW; PlantNET

Soliva sessilis

Florabase; KEW; PlantNET; McIntyre et al 1995; Lovell et al 1986

Sonchus asper

Florabase; KEW; PlantNET; Google images

Sparganium subglobosum

Florabase; KEW; PlantNET

Stellaria flaccida

Florabase; KEW; PlantNET; Miller and West 2012

Stellaria media

Florabase; KEW; PlantNET; Grundy et al 2003

Stephania japonica

Florabase; KEW; PlantNET; Clifford 2000

Syzygium australe

ATRP; Florabase; KEW; PlantNET; Clifford 2000

Tagetes minuta

Florabase; KEW; PIER; PlantNET; Google images;

Tradescantia fluminensis

Florabase; KEW; PlantNET

Trema tomentosa

Florabase; KEW; PlantNET

Trifolium arvense

ATRP; Florabase; KEW; PlantNET;Barclay and Earle 1974; Felfoldi 1980; Grime et al 1981; Matlack 1987

Trifolium dubium

Florabase; KEW; PlantNET; Google images

Trifolium glomeratum

Florabase; KEW; PlantNET

Trifolium repens

Florabase; KEW; PlantNET; Moles et al 2003

Tristaniopsis laurina

FloraBase; PlantNET; Sweedman and Merritt 2006; Chong et al 2007

Urtica urens

Florabase; KEW; PlantNET; Grime et al 1981

Urtica incisa

ATRP; Florabase; KEW; OSUWeeds; PlantNET; Google images

Verbena bonariensis

ATRP; Florabase; KEW; PlantNET; UQLD; Ganzaugh 1980

Veronica persica

Florabase; KEW; PlantNET; Grundy et al 2003

Veronica plebeia

ATRP; FloraBase; PlantNET; RBGDT

Viola hederacea

ATRP; Florabase; KEW; PlantNET; ATRP

Vulpia muralis

Florabase; KEW; PlantNET

Vulpia myuros

Florabase; KEW; OSU; PlantNET; Google images

Wahlenbergia communis

Florabase; KEW; PlantNET; RBGDT

Wahlenbergia gracilis

Florabase; KEW; PlantNET; RBGDT; Google images; Moles et al 2000

Xanthorrhoea latifolia subsp. Latifolia

Florabase; KEW; PlantNET; Borsboom 2005

APPENDIX 3 – Species trait data with information sources
PART C - Internet resources and databases

ABRS

Australian Biological Resouorces Study (ABRS). 2007. Flora of Australia Volume 2. Commonwealth of Australia
http://www.anbg.gov.au/abrs/online-resources/flora/main-query-styles.html

AustWC

Australian Weeds Committee. 20??. Weeds Australia – An Australian Weeds Committee National Initiative. Weed Identification Tool. Australian State and Territory Governments.
http://www.weeds.org.au/

ATRP

CSIRO. 2010. Australian Tropical Rainforest Plants, Edition 6 – Trees, Shrubs, Vines, Herbs, Grasses, Sedges, Palms, Pandans & Epiphytes. Version 6.1, December 2010.
http://www.anbg.gov.au/cpbr/cd-keys/rfk/

PlantNET

Botanic Gardens Trust. 2012. PlantNET - The Plant Information Network System of The Royal Botanic Gardens and Domain Trust, Sydney, Australia (version 2.0).
http://plantnet.rbgsyd.nsw.gov.au.

CSIROtrop

Tropical Forages: An Interactive Selection Tool. 2005. CSIRO Sustainable Ecosystems (CSIRO), Department of Primary Industries and Fisheries (DPI&F Queensland), Centro Internacional de Agricultura Tropical (CIAT) and International Livestock Research Institute (ILRI).
http://www.tropicalforages.info/key/Forages/Media/Html/index.htm

Florabank

Greening Australia. 20??. Florabank. Australia's premier resource for native seed. Factsheets. Australian Government, Greening Australia and CSIRO.
http://www.florabank.org.au/lucid/key/species%20navigator/media/html/index.htm

Florabase

Western Australian Herbarium. 1998–2015. FloraBase—the Western Australian Flora. Department of Parks and Wildlife.
https://florabase.dpaw.wa.gov.au/

FNWDUS

Center for Plant Health Science and Technology (CPHST). 2010. Federal Noxious Weed Disseminules of the U.S - Edition 2.1. Center for Plant Health Science and Technology and California Department of Agriculture (CDFA)
http://itp.lucidcentral.org/id/fnw/key/Whole_key_html/Taxalist_factsht.htm

GISD

Invasive Species Specialist Group. 2010. Global Invasive Species Database. Standard Search (*Delairea odorata*). Invasive Species Specialist Group (ISSG) of the SSC - Species Survival Commission of the IUCN - International Union for Conservation of Nature.
http://www.issg.org/database/species/ecology.asp?si=1187

APPENDIX 3 – Species trait data with information sources

PART C - Internet resources and databases

Google images

Google image search.
https://images.google.com/

HerbiGuide

HerbiGuide. 1988-2014. The Pesticide Expert on a Disk. Herbiguide Pty Ltd.
http://www.herbiguide.com.au/InformationWeeds.aspx

PIER

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http://www.hear.org/pier/index.html

KEW

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NSWOEH

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OSU

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OSUWeeds

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http://www.rbgsyd.nsw.gov.au/science/Evolutionary_Ecology_Research/Ecology_of_Cumberland_Plain_Woodland/woodland_plants

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http://sydneyweeds.org.au/about/what-is-this-weed/

TasDPIPWE

APPENDIX 3 – Species trait data with information sources

PART C - Internet resources and databases

Tasmanian Threatened Species Listing Statement, Threatened Species Section – Tasmanian Department of Primary Industries, Parks, Water and Envrionment.
http://dpipwe.tas.gov.au/conservation/threatened-species/lists-of-threatened-species/threatened-species-vascular-plants/threatened-species-list-vascular-plants-a-b

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APPENDIX 4

Results of seedling emergence study 1

Link to .csv file:

https://drive.google.com/open?id=0Byfdvrg9IkecY0J2U2xJU296RUk

Link to .xslx file:

https://drive.google.com/open?id=0Byfdvrg9IkecV1pPZ0xlemhZaUk

APPENDIX 5

Results of seedling emergence study 2

Link to .csv file:

https://drive.google.com/open?id=0Byfdvrg9IkecOV9JSnJMM3N0czg

Link to .xslx file:

https://drive.google.com/file/d/0Byfdvrg9IkecNDhJSGYzNVNpVlk/view?usp=sharing

APPENDIX 6

Vegetation survey results

Link to .csv file:

https://drive.google.com/file/d/0Byfdvrg9IkecZU5TYWZCSy1uWlk/view?usp=sharing

Link to .xslx file:

https://drive.google.com/file/d/0Byfdvrg9IkecM3RWdjVid0NENms/view?usp=sharing

APPENDIX 7

Supplementary information tables for O'Donnell et al 2016 (chapter 5)

Table S1. Desirability criteria and analysis techniques used to assess the geomorphic condition of rivers in the Wollombi-Watagan catchment. Based on Brierley and Fryirs (2005)

Degrees of freedom Geoindicators	Questions to ask for each reach of the River Style	Analysis Techniques (see Brierley and Fryirs, 2005)	Some key indicators and expectations in the field DESIRABILITY CRITERIA	No. of criteria that must be answered YES to receive a tick (see Table 2)
Channel attributes 1. Size 2. Shape 3. Bank morphology 4. Woody debris loading 5. Instream vegetation structure	1. Is channel size appropriate given the catchment area, the prevailing sediment regime and the vegetation character such that the channel and floodplain are functionally connected? 2. Is channel shape appropriate along the reach? 3. Are banks eroding in the right places and at the right rate? 4. Is there woody debris in the channel and/or potential for woody debris recruitment? 5. Is the instream vegetation structure appropriate?	1. Width-depth ratio and cross-sectional area of the channel relative to the catchment area it drains 2. Identification of irregular, compound, symmetrical or asymmetrical channels 3. Identification of uniform vertical, uniform graded, faceted, undercut banks and characterisation of bank texture using grain size analysis 4. Qualitative rating of type, alignment and abundance of wood in channel 5. Qualitative rating of the composition (native versus exotic) and coverage of vegetation on instream geomorphic surfaces	1. Narrow, deep channel with benches stabilised by vegetation. 2. Symmetrical or compound channel at inflection points and asymmetrical at bends. 3. Concave bank erosion but not bank slumping or channel expansion. 4. Wood-induced pools present. 5. Dominantly native vegetation acting to increase geo-diversity and stability of sand-bed, banks and bank-attached geomorphic units	**4 OUT OF 5**
River planform 6. Lateral channel stability 7. Assemblage of geomorphic units 8. Riparian vegetation	6. Is the lateral stability of the channel appropriate given the texture and slope of the reach? 7. Is the assemblage, pattern and condition of instream and floodplain geomorphic units appropriate? Are key units present? 8. Is the continuity and composition of the riparian zone near-natural, with few exotics?	6. Identification of channel expansion, bank erosion and avulsion processes 7. Analysis of form and sedimentology to interpret processes responsible for formation of units, assessment of the juxtaposition and assemblage of units, assessment of channel-floodplain connectivity and unit condition (signs of reworking, dissection) 8. Qualitative rating of the composition (native versus exotic), continuity, and structure of vegetation assemblages in the riparian zone	6. NO signs of instability such as macrochannel expansion, low flow channel reworking of bed materials. 7. Diverse range of units including bedrock or wood-induced pools, vegetation induced riffles, sand bars, benches and floodchannels/backswamps. No signs of degradation e.g. homogenous sand sheets in the channel (slugs) and on the floodplain. 8. Diverse and dominantly native riparian corridor.	**2 OUT OF 3**
Bed character 9. Bed stability 10. Hydraulic diversity 11. Sediment regime	9. Is bed stability appropriate? 10. Are roughness characteristics and the pattern of hydraulic diversity along the reach appropriate? 11. Is the sediment storage/transport function of the reach appropriate for the catchment position	9. Interpretation of vertical bed activity via incision 10. Visual water surface flow estimates 11. Identifying sediment process zone (i.e. source, transfer, accumulation) and quantitative measure of sediment transport capacity versus sediment availability to interpret supply versus transport limited reaches	9. No signs of bed instability or disturbance e.g. incision into sand bed materials, aggradation of sand sheets or formation of multiple thalwegs in sand slugs. 10. Channels and associated geomorphic units shaped by vegetation and wood. Diversity of hydraulic flow characteristics. 11. Reach acts as sediment transfer zone, not accumulation or source zones. Transfer zones evidenced by bar-to-bar sediment transfer. Accumulation zones are evidenced by sand sheets and slugs.	**2 OUT OF 3**

Table S2. a) The requirements for determination of geomorphic condition of river reaches using the River Styles framework (from Brierley and Fryirs 2005). b) Results of the geomorphic condition assessment as applied to the seven river reaches - Will O Wyn (WOW), Murrays Run (MR) and Laguna (L) situated along Wollombi Brook; Watagan State Forest (WSF), Upper Watagan (UW) and Mid Watagan (MW) situated along Watagan Creek; and a reach at Dairy Arm (DA) - based on the desirability criteria outlined in Table 1. Final condition (P) poor, (ML) moderate lower, (MU) moderate upper, (G) good.

a)

Geomorphic river condition	**Requirements across the three degrees of freedom**
Good	Needs three ticks
Upper Moderate	Needs two ticks and one cross
Lower Moderate	Needs two crosses and one tick
Poor	Needs three crosses

b)

Degree of freedom (DF) for each geoindicator	**Desirability criteria (Table 1)**	**Study reaches**						
		DA	**L**	**MR**	**MW**	**UW**	**WOW**	**WSF**
Channel attributes	1.	X	✓	✓	✓	X	X	✓
	2.	✓	✓	X	✓	✓	✓	✓
	3.	X	✓	✓	✓	✓	✓	✓
	4.	X	X	X	✓	✓	✓	✓
	5.	X	X	X	X	✓	✓	✓
River planform	6.	X	✓	✓	✓	✓	✓	✓
	7.	X	X	X	X	✓	✓	✓
	8.	X	X	X	X	✓	✓	✓
Bed character	9.	X	✓	✓	✓	✓	✓	✓
	10.	X	✓	X	✓	✓	✓	✓
	11.	X	✓	✓	✓	✓	✓	✓
Achievement of DF		XXX	XX✓	XX✓	✓X✓	✓✓✓	✓✓✓	✓✓✓
Condition		P	LM	LM	UM	G	G	G

Table S3. Summary of results from the Rapid Appraisal of Riparian Condition (Jansen *et al.*, 2005). Results for the seven study reaches: Will O Wyn (WOW), Murrays Run (MR) and Laguna (L) situated along Wollombi Brook; Watagan State Forest (WSF), Upper Watagan (UW) and Mid Watagan (MW) situated along Watagan Creek; and a reach at Dairy Arm (DA). Data for each reach shows the average measurements and scores based on four survey transects.

HABITAT: Longitudinal continuity and width of riparian canopy vegetation; proximity to native vegetation patrch>10Ha

Longitudinal Continuity: 0 = <50%, 1 = 50-64%, 2 = 65-79%, 3 = 80-94%, 4 = ≥95% vegetated bank; with ½ point subtracted for each significant discontinuity (>50m long)

Width: *Channel ≤10m wide:* 0 = VW <5m, 1 = VW 5-9m , 2 = VW 10-19m, 3 = VW 20-39m, 4 = VW ≥40m

Channel >10m wide: 0 = VW/CW<0.5, 1 = VW/CW 0.5-0.9, 2 = VW/CW 1-1.9, 3 = VW/CW 2-3.9, 4 = VW/CW ≥4

Nearest patch of native vegetation >10ha: 0 = >1km, 1 = 200m-1km, 2 = contiguous, 3 = contiguous with patch >50ha

	Longitudinal Continuity	Channel Width (CW)	Vegetation Width (VW)	Score	Proximity to native veg patch
DA	-0.5	20	0	0	1
L	1	14	1	1	1
MR	1	10.75	1	1	2
MW	1	13	1	0.75	1
UW	2	11	2.25	2.25	3
WOW	2	15.5	4	4	3
WSF	3	14.75	3.5	3.5	3

COVER & NATIVES: Vegetation cover: Canopy >5m, Understorey 1-5m, Ground cover <1m

Canopy and ground cover: 0 = none, 1 = 1-30%, 2 = 31-60%, 3 = >60%

Understorey cover: 0 = none, 1 = 1-5%, 2 = 6-30%, 3 = >30%

	Canopy	Native canopy	Understorey	Native understorey	Ground cover	Native ground cover	# layers
DA	0.25	0.25	0.75	0.5	2.5	1.25	1.5
L	1	1	1	0.75	2.25	1.5	3
MR	1	1	1	0.5	2.75	1.25	2
MW	1.25	1.25	0.5	0.5	2.5	1.5	3
UW	1	1	2.5	2.5	2	1	3
WOW	2.5	2.5	2.75	2.5	2.5	2.5	3.75
WSF	2.5	2.75	2.25	2.25	1	1	2.75

Continued

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DEBRIS

Leaf litter & native leaf litter cover: 0 = none, 1 = 1-30%, 2 = 31-60%, 3 = >60%

Standing dead trees (>20cm dbh) & hollow-bearing trees: 0 = absent, 1 = present

Fallen logs (>10cm diameter): 0 = none, 1 = small quantities, 2 = abundant

	Leaf litter	Native leaf litter	Standing dead trees	Hollow-bearing trees	Fallen logs
DA	0.5	0.5	0.25	0	0.25
L	1	1	0.75	0.5	0.75
MR	1	1	0.75	0	1.5
MW	1.25	1.25	0.25	0.75	1.25
UW	1	1	1	0.75	2
WOW	2.5	2.5	0.75	0	1.5
WSF	2	2	0.5	0.5	2

FEATURES

Regeneration <1m tall: 0 = none, 1 = scattered, and 2 = abundant, with ½ point subtracted for grazing damage

Reeds & large tussock grasses: 0 = none, 1 = scattered, and 2 = abundant

	Native canopy species regeneration	Native understorey regeneration	Large native tussock grasses	Reeds
DA	0.25	0.25	1	0
L	0.75	0.75	1.25	0.75
MR	0.75	0	1.5	0.75
MW	0.5	1	1.25	0.25
UW	1	1.5	0.5	0
WOW	1	1.5	1.25	0.75
WSF	1.5	0.75	1.75	0

TOTAL SCORES

	Habitat	Cover	Natives	Debris	Features	**Total (/50)**	**Grading**
DA	0.5	5	2	1.5	1.5	**10.5**	**very poor**
L	3	7.25	3.25	4	3.5	**21**	**very poor**
MR	4	6.75	2.75	4.25	3	**20.75**	**very poor**
MW	2.75	7.25	3.25	4.75	3	**21**	**very poor**
UW	7.25	8.5	4.5	5.75	3	**29**	**Poor**
WOW	9	11.5	7.5	7.25	4.5	**39.75**	**Good**
WSF	9.5	8.5	6	7	4	**35**	**Good**

Table S4. Final determination of overall riparian condition assessment based on the combined scores of the River Styles geomorphic condition assessment and the Rapid Appraisal of Riparian Condition. Final condition (P) poor, (LM) lower moderate (UP) upper moderate, (G) good.

Assessment scores	DA	L	MR	MW	UW	WOW	WSF
River Styles (/11)	1	7	5	8	10	10	11
River Styles converted (/50)	4.5	31.82	22.72	36.36	45.45	45.45	50
RARC (/50)	10.5	21	20.75	21	29	39.75	35
Combined score (/100)	15	52.82	43.47	57.36	74.45	85.2	85
Final assessment of riparian condition	P	LM	LM	LM	UM	G	G