

# The potential of soil seed banks of a eucalypt wetland forest to aid restoration

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**Abstract** Soil seed banks can play an important role in the regeneration of wetland vegetation. However, their potential role in the restoration of degraded wetland forests is less certain. I surveyed the soil seed bank and extant floras of four sites across a eucalypt wetland forest of variable vegetation condition. At each site, the extant vegetation was surveyed within two  $5 \times 5 \text{ m}^2$  quadrats, each from which five composite soil seed bank samples were collected. Across the four sites, 57 (including 18 exotic) species were identified in the extant vegetation, while from the seed bank samples 6379 seedlings emerged from 80 taxa, 33 of which were exotic species. The soil seed bank was dominated by native and exotic monocots, and contained very few seeds of wetland tree or shrub species. Overall, the similarity between the extant and seed bank floras was very low ( $\sim 24\%$ ). Soil seed banks are likely to be of limited use in the restoration of degraded wetland *forests*, because the dominant species in such systems—woody and clonal plants—are typically absent from the soil seed bank. Wetland soil seed banks may contribute to the maintenance and diversity of understorey vegetation, however, they may also act as a source of exotic plant invasions, particularly when a wetland is degraded.

**Keywords** Exotic plant invasion · Soil seed bank · Swamp forest · Vegetation cycling · Wetland restoration

## Introduction

Soil seed banks confer resilience to wetland plant communities by allowing species-rich communities to persist during dry times and to recover rapidly following re-wetting (Brock et al. 2003; Capon and Brock 2006). Soil seed banks also play an important role in the cycling of wetland vegetation during hydrological fluctuations (van der Valk and Davis 1978; Brock and Casanova 1997) and may support geomorphic recovery of degraded riparian zones through vegetation regeneration (O'Donnell et al. 2016). Nonetheless, studies that have considered the potential role of soil seed banks in wetland restoration have reached mixed conclusions. While some studies of wetlands have reported diverse seed bank floras appropriate for aiding restoration activities (Richter and Stromberg 2005; Nishihiro et al. 2006; James et al. 2007; Li et al. 2008; Baldwin et al. 2010; Tererai et al. 2015), other studies have found seed banks lacking in target species for restoration (Middleton 2003; Lu et al. 2010; Kettenring and Galatowitsch 2011). Conversely, other studies have suggested that the restoration of degraded environments, including wetlands, may be hampered by soil seed banks due to the

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prevalence of exotic plant propagules (Williams et al. 2008; Eldridge and Lunt 2010).

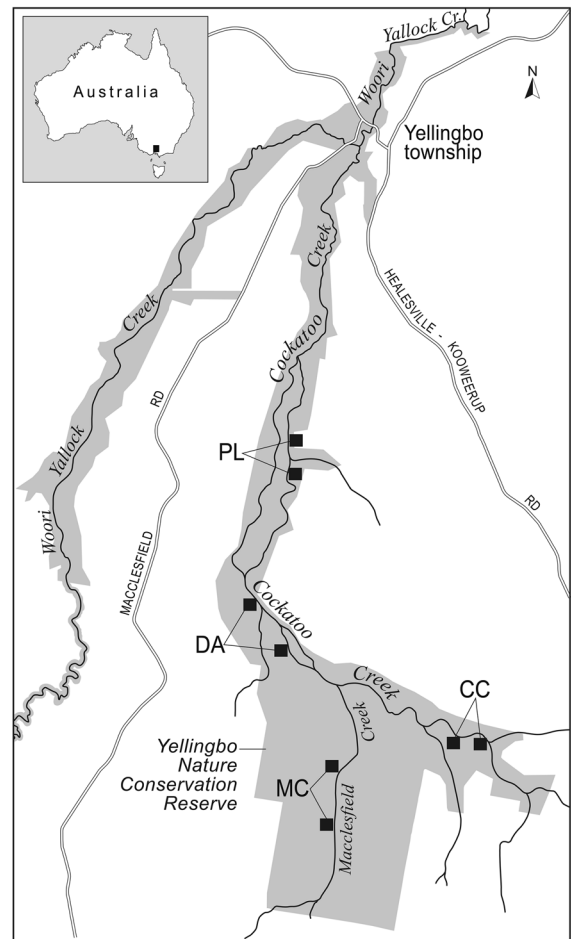
It has been suggested that seed banks are important for the development of some components of the vegetation, but not others (Boedeltje et al. 2003). Indeed, woody wetland plant species are often poorly represented in the soil seed bank and reliant on alternative means of regeneration (Middleton 2003); the potential of the soil seed bank to contribute to the restoration of herbaceous vegetation may be greater (Boudell and Stromberg 2008; O'Donnell et al. 2016). Understanding the similarity of species composition between the seed bank and extant vegetation (which for wetlands can vary greatly ~20–80 %), can provide insights into the role of the seed bank in vegetation dynamics at a site, and thus its potential role in restoration (Hopfensperger 2007).

The purpose of the current study was to assess the utility of the soil seed bank for the restoration of eucalypt wetland forests of critical importance. These wetland forests, home to two critically endangered arboreal fauna, are in demonstrable decline and the target of considerable restoration efforts. With hydrological works planned aimed at naturalising water regimes and restoring forest habitat (through both improved condition of existing forests and promoting regeneration), the potential role of the soil seed bank to facilitate wetland forest regeneration required assessment. Accordingly, this study sought to answer: what was the composition of the soil seed bank in relation to the (1) extant vegetation? And (2) in relation to extant vegetation condition? And hence, what was the potential role of the soil seed bank in the maintenance and restoration of these critically important wetland forests?

## Methods

### Study area

This study focused on the wetland forests of the Yellingbo Nature Conservation Reserve, which is located ~50 km east of Melbourne, SE Australia (Fig. 1). The reserve was gazetted in 1965 to protect the helmeted honeyeater (*Lichenostomus melanops cassidix*), and consists of narrow sections of remnant riparian forest (bounded by cleared agricultural land) along parts of several creeks. As well as the critically



**Fig. 1** Study site locations within the Yellingbo Nature Conservation Reserve where the extant vegetation and soil seed bank were surveyed. Labels indicate different sites, black squares indicate survey locations

endangered helmeted honeyeater, the reserve also supports a genetically distinct and only known lowland population of the critically endangered Leadbeater's possum (*Gymnobelideus leadbeateri*) (Harley et al. 2005). Both these arboreal fauna species are strongly associated with *Eucalyptus camphora* (mountain swamp gum) forest/woodland and associated shrub thickets, which predominate in the wetter areas of the reserve adjacent to the Cockatoo and Macclesfield Creeks. These wetland forests comprise an understorey rich in sedges, are seasonally to near permanently inundated/waterlogged (Pearce and Minchin 2001) and are collectively known as the 'Cockatoo Swamp'. This 'sedge-rich *E. camphora* swamp community' is threatened by extensive tree and shrub dieback and a lack of woody plant regeneration

(Turner 2003), probably because of the result of hydrological alteration (with some riparian areas currently disconnected from the creeks by levees, and others suffering from prolonged waterlogging) (Greet 2015).

### Sampling design

I surveyed the extant vegetation and soil seed bank at four sites across the Yellingbo Nature Conservation Reserve (Fig. 1). These sites were all within mature *E. camphora* swamp forest/woodland and were selected so that they were spatially distributed across the Cockatoo Swamp, and represented a range of overstorey and understorey vegetation conditions. One site was established on the Macclesfield Creek floodplain (Site MC) in an area with healthy overstorey and intact native understorey. The other three sites, CC, DA and PL, were located on the Cockatoo Creek floodplain. Site CC was semi-cleared with an understorey heavily invaded by exotics (with *Holcus lanatus* and *Ranunculus repens* particularly abundant). Site DA was in an area subject to prolonged waterlogging with dieback affected trees and shrubs yet an intact understorey. Site PL was established in an area with healthy overstorey, but moderately disturbed understorey vegetation. Thus, two of the four sites had healthy overstorey (MC and PL), and two sites had intact understorey (MC and DA).

### Sampling

I surveyed the extant vegetation and collected soil seed bank samples in August (late winter) 2012. Firstly, two  $5 \times 5$  m<sup>2</sup> quadrats were randomly established at each site. For each quadrat, the estimated projective foliage cover of all extant plant species identified was recorded (to the nearest 5 %), and five randomly located soil seed bank samples were collected. Each seed bank sample comprised five replicate cores taken to a depth of 5 cm using a soil augur of 5 cm diameter. Thus, 40 composite seed bank samples (4 sites  $\times$  2 quadrats  $\times$  5 samples) were collected. Soil seed bank samples were dried and their composition determined using the seedling emergence (or ‘grow out’) method (Poiani and Johnson 1988; Gross 1990). Specifically, dried samples were spread evenly (to  $\sim$ 5 mm depth) over seedling trays filled with moistened sterile seed raising media. Control trays with media but without

seed bank material were used to monitor for contamination (none was observed). Trays were placed randomly within a glasshouse wherein temperatures were maintained between 16–18 °C at night and 23–25 °C during the day, and samples kept moist via mist irrigation—conditions considered appropriate for the germination of the vast majority of Australian wetland plant species (Brock et al. 1994; Casanova and Brock 2000). Emergent seedlings were identified to species level and removed. When necessary, seedlings were potted up to facilitate flowering and identification. Samples were discarded after no further germinants were observable ( $\sim$ 4–6 months).

### Data analysis

For analyses, all taxa were identified to species level, except in the case of two grass seed bank taxa. For the seed bank taxa, numbers of taxa, as well as seedling abundances were determined for taxa grouped according to origin (native or exotic), growth form (monocot, forb, or woody), and life-span (annual/biennial or perennial). Species recorded in the extant vegetation were grouped similarly. For the seed bank taxa, differences in species richness and seedling abundances for the various plant groupings were assessed using ANOVAs with site as a fixed factor and quadrat as a random factor nested within site. For significant site differences, differences between site means were assessed using a Tukey’s HSD test. For all univariate tests, residuals were examined to ensure they fulfilled the assumptions of normality and homogeneity of variance, and data square-root transformed where necessary, i.e. for all seedling abundance analyses.

Two-dimensional non-metric multidimensional scaling (NMDS; Kruskal and Wish 1978), permutational MANOVA (PERMANOVA; Anderson 2001), hierarchical cluster analyses, and similarity percentage (SIMPER; Clarke and Gorley 2001) analyses were conducted using the Bray–Curtis dissimilarity measure in Primer v6 to examine assemblage-level differences between the extant and seed bank floras. For the PERMANOVA, Flora type (extant or seed bank) and site were treated as fixed factors, with quadrat nested within site included as a random factor. Indicator value analysis was conducted using the *indicspecies* package in R to determine species associations with either the extant and seed bank floras (De Caceres and Legendre 2009). All species

were included and assemblage data transformed to presence/absence for all multivariate analyses.

## Results

### Extant vegetation

Fifty-seven species were recorded in the extant vegetation across the four sites, of which more than two-thirds (39) were native (Table 1). Almost all native species were perennials, while half of the 18 exotic species were annual or biennial species. The surveyed vegetation included nine woody species (of which the blackberry, *Rubus anglocandicans*\*, was the only exotic; N.B. asterisks are used hereafter to denote exotic species). *E. camphora* and *Carex appressa* were the most frequently observed species, occurring in 7 out of the 8 quadrats, with *Phragmites australis*, *Melaleuca squarrosa*, and *Baumea rubiginosa* also common (see Table 3 in Appendix 1 for full list of surveyed species).

### Seed bank flora

A total of 6379 seedlings emerged from the soil seed bank samples. These were from 80 different taxa, including 45 native and 33 exotic species (Table 1). The four most common species were all *Juncus* species: *J. bufonius* (963 seedlings), *J. bulbosus*\* (742), *J. articulatus*\* (666), and *J. planifolius* (647). Together these four species accounted for almost half of all seedlings—and none were recorded in the extant vegetation. Native trees and shrubs accounted for only 28 seedlings representing six species; no *E. camphora* or *M. squarrosa* seedlings emerged from the seed bank samples. Most seed bank taxa were represented by

only a relatively small number of seeds (see Table 4 in Appendix 2 for full list of seed bank taxa).

### Similarity between the extant and seed bank floras

Twenty-four species, including three exotic and two annual species, were found solely in the extant vegetation (and not in the seed bank). Conversely, 47 species, including 18 exotic and 15 annual/biennial species, were found solely in the seed bank. Fourteen species from a range of growth forms were significantly associated with the extant vegetation, including three woody species (Table 2). Six species were significantly associated with the seed bank flora, five of which were monocots, none were woody and two were exotic (Table 2). There were no species associated with both. Overall, the similarity between the extant and seed bank floras was very low (average similarity ~24 % across all sites). Correspondingly, the ordination separated the extant vegetation and seed bank data, and this difference between the extant and seed bank floras was significant;  $p = 0.009$ . While hierarchical cluster analyses grouped most of the extant vegetation data and seed bank sample data separately in two large clusters, it grouped both the extant and seed bank floras of site CC in a third separate cluster (at the 25 % similarity level; Fig. 2).

### Relationship between seed bank composition and extant vegetation condition

There were significant differences between the seed bank floras of the different sites, with sites with more disturbed understorey vegetation tending to have seed banks with fewer native and more exotic species (Fig. 3). The average cover of exotic understorey species recorded in quadrats at sites MC (0.5 %) and

**Table 1** Total numbers of taxa that were surveyed in the extant vegetation and that emerged from seed bank samples collected across all four sites

	Extant vegetation			Seed bank flora		
	Native	Exotic	Total	Native	Exotic	Total
Species richness	39	18	57	45	33	80
Annuals/biennials	2	9	11	7	17	24
Perennials	37	9	46	38	16	53
Monocots	18	3	21	19	9	29
Forbs	12	14	26	20	23	43
Woody	8	1	9	6	1	7

**Table 2** Species significantly associated with either the extant or seed bank floras determined by indicator species analyses

Species	Origin	Growth form	Life-span	Specificity	Frequency	Stat	<i>p</i>
Species associated with the extant vegetation							
<i>Eucalyptus camphora</i>	Native	Woody	p	1	0.875	0.935	0.001
<i>Phragmites australis</i>	Native	Monocot	p	1	0.625	0.791	0.001
<i>Melaleuca squarrosa</i>	Native	Woody	p	1	0.5	0.707	0.002
<i>Baumea rubiginosa</i>	Native	Monocot	p	1	0.5	0.707	0.001
<i>Persicaria praetermissa</i>	Native	Forb	p	1	0.375	0.612	0.003
<i>Tetrarrhena juncea</i>	Native	Monocot	p	1	0.375	0.612	0.006
<i>Gahnia radula</i>	Native	Monocot	p	1	0.375	0.612	0.006
<i>Schoenus lepidosperma</i>	Native	Monocot	p	1	0.375	0.612	0.005
<i>Galium aparine</i>	Exotic	Forb	a	0.94	0.375	0.593	0.01
<i>Prunella vulgaris</i>	Exotic	Forb	p	0.88	0.375	0.575	0.032
<i>Gonocarpus humilis</i>	Native	Forb	p	0.88	0.375	0.575	0.026
<i>Coprosma quadrifida</i>	Native	Woody	p	1	0.25	0.5	0.03
<i>Triglochin procera</i>	Native	Forb	p	1	0.25	0.5	0.024
<i>Ranunculus inundatus</i>	Native	Forb	p	1	0.25	0.5	0.032
Species associated with the seed bank							
<i>Juncus bufonius</i>	Native	Monocot	a	1	0.8	0.894	0.001
<i>Juncus planifolius</i>	Native	Monocot	a	1	0.775	0.88	0.001
<i>Juncus procerus</i>	Native	Monocot	p	0.875	0.875	0.875	0.001
<i>Juncus articulatus</i>	Exotic	Monocot	p	1	0.575	0.758	0.009
<i>Juncus bulbosus</i>	Exotic	Monocot	p	1	0.5	0.707	0.038
<i>Gratiola pubescens</i>	Native	Forb	p	1	0.475	0.689	0.04

Species characteristics presented are origin (native or exotic), growth form (monocot, forb or woody), and life-span (a—annual, p—perennial). Specificity = affinity to a flora type, i.e. a specificity of 1 means that species was solely found in that flora type. Frequency = proportion of samples of that flora type in which that species was present. Stat = test statistic. *p* = significance level

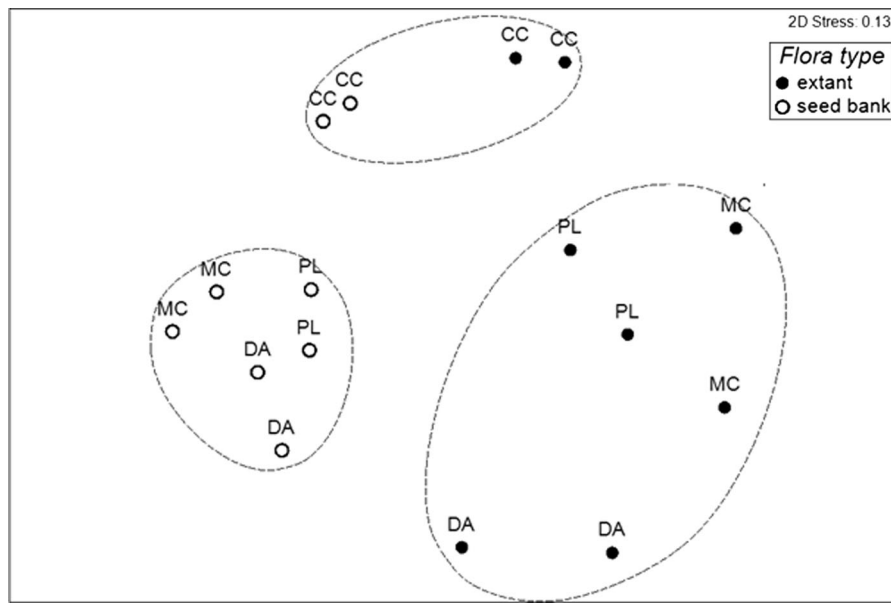
DA (3 %) was much less than at sites PL (60 %) and CC (95 %). Correspondingly, native species richness of the seed bank was greatest for one of the less disturbed sites, site DA, and least for the most disturbed site, site CC ( $p = 0.039$ ). Conversely, the two most disturbed sites tended to have greater exotic species richness ( $p = 0.096$ ) and exotic species seedling abundance ( $p = 0.049$ ). Patterns between overstorey condition and seed bank composition were not apparent.

## Discussion

Overall, the soil seed bank and extant floras of the wetland forests surveyed were dissimilar. In particular, very few woody plant seedlings or seedlings from the dominant extant species were recovered from the soil seed bank. The soil seed bank did

contain a diversity of native herbaceous plant species, however, it was largely dominated by a few monocot species, and in some cases contained marked numbers of exotic species—comparatively many more than in the extant vegetation—particularly at disturbed sites.

Soil seed banks tend to be dominated by pioneer species—those adapted to readily colonise disturbed areas (i.e. ruderals *sensu* Grime 1977). Ruderal species tend to be short-lived, i.e. annual or biennial species, produce large numbers of seeds, and several studies have found wetland seed banks to be dominated by such species (Capon and Brock 2006; Lu et al. 2010; O'Donnell et al. 2014). However, some studies have found wetland perennials to also be common in the soil seed bank (Richter and Stromberg 2005; Williams et al. 2008), as was found in this study (e.g. *Carex appressa* which was common in the extant vegetation and was also well represented in the seed bank).



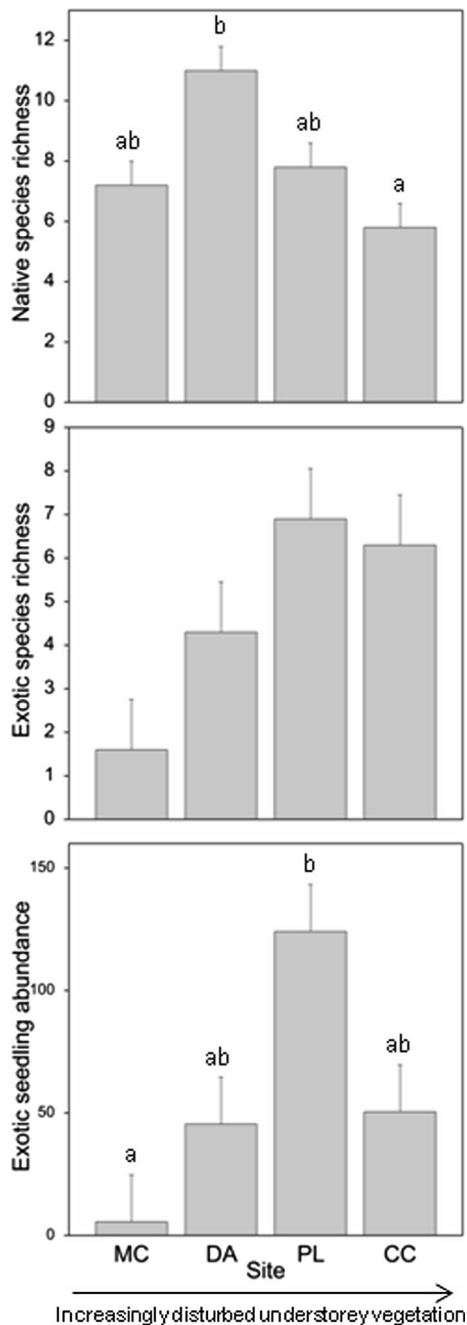
**Fig. 2** NMDS ordination of the extant and seed bank floras based on the quadrat survey and seed bank sample data (averaged at the quadrat-level) respectively; labels indicate site. Dashed ovals represent hierarchical cluster groupings at the 25 % similarity level

Ruderal species tend to produce large numbers of small seeds that are highly mobile (readily dispersed by wind or water), and many are successful invaders of degraded native vegetation communities (i.e. exotics). Indeed, seed banks often contain considerable numbers of exotics (Williams et al. 2008; O'Donnell et al. 2014). Furthermore, degraded wetland areas are likely to have seed banks with an enhanced prevalence of exotics (Williams et al. 2008; Greet et al. 2012; O'Donnell et al. 2016). Thus, degradation can lead to increased similarity of extant and seed bank floras as both become dominated by weedy vegetation (Gioria and Osborne 2009). Similar findings were made in the current study, with greater numbers of annual/biennial species, and almost twice as many exotics recorded in the seed bank compared to the extant vegetation. Furthermore, this pattern was more pronounced in more degraded sites, sites at which the similarity of the extant and seed bank floras was greatest.

Many herbaceous perennial wetland plants rely on vegetative reproduction rather than reproduction from seed. Such clonal species—more common in permanently moist than in ephemeral wetland environments—can be expected to be largely absent from the soil seed bank (Abernethy and Willby 1999; Hopfensperger 2007). Indeed, in this study, clonal species that

were dominant in the understorey such as *Phragmites australis*, *Baumea rubiginosa*, and *Gahnia radula*, were absent from the soil seed bank. Together, the lack of woody and clonal species in wetland seed banks accounts for their general lack of similarity with the extant floras of wetland environments (Thompson and Grime 1979; Boedeltje et al. 2003). This dissimilarity could be expected to be particularly pronounced in wetland forests (i.e. swamps), which are dominated by woody vegetation and tend to be more permanently moist and thus favourable to plants that reproduce vegetatively. However, this dissimilarity could be expected to be reduced following a major disturbance, e.g. flood or fire, when significant germination from the soil seed bank could be expected (Capon and Brock 2006; Hopfensperger 2007).

The absence of a sizeable woody soil seed bank is typical of wetland environments (Leck and Graveline 1979; Schneider and Sharitz 1986; Middleton 2003; Lu et al. 2010). Woody wetland plants often release seeds that are non-dormant (germinate readily) and/or viable for only a short period of time. Thus, rather than a persistent soil seed bank, woody wetland plants depend on other reproductive strategies including: seed release periods timed to coincide with favourable hydrological conditions (Mahoney and Rood 1998;



**Fig. 3** Associations between seed bank flora composition and sites, with sites shown in order of increasingly disturbed understorey vegetation. Fitted means with *standard error bars* presented. Significant differences between site means determined by post hoc Tukey's HSD tests indicated by *lower case letters*

Pettit and Froend 2001); vegetative reproduction (e.g. willows; Stokes and Cunningham 2006); or serotiny—i.e. the storage of seeds in their canopy, seeds which

are then released *en masse* following a significant disturbance such as a flood or fire (Jensen et al. 2008; Hamilton-Brown et al. 2009). The dominant tree of the wetland forests studied, *E. camphora*, exhibits all these traits, i.e.: its seeds germinate readily; it releases a pulse of seeds in late spring/early summer; forms new trees via the epicormic growth of fallen trees; and stores seed in its canopy (Greet 2015). Woody co-dominants such as *Melaleuca squarrosa* and *Leptospermum lanigerum* behave similarly. While the soil seed bank was only sampled on one occasion for this study (and at a time not correlated with the *peak* seed release timing of the woody dominants), a steady background seed rain is observed in seedfall traps, and other soil bank assays at the site have similarly revealed a lack of woody plant propagules (Michelle Faram, pers. comm.).

#### Role for wetland seed banks in wetland forest restoration?

Many authors who have found species-rich wetland seed banks have promoted their potential to drive vegetation recovery following the removal of a degrading pressure (e.g. inappropriate water regime or plant invasion), or even their use as a donor seed bank for the restoration of nearby degraded areas (Richter and Stromberg 2005; Li et al. 2008; Tererai et al. 2015). It is possible that wetland soil seed banks in such situations could contribute to the diversity of understorey vegetation. Indeed, in the wetland forest system we studied, the soil seed bank is likely to contribute to the maintenance of some native herbaceous plant populations (e.g. *Carex appressa*) and the species richness of the site.

However, wetland seed banks are only likely to be useful for restoring some components of the vegetation community, primarily for supporting early stages of succession via the regeneration of pioneer plants (Leyer 2006; Vosse et al. 2008). The very low similarity recorded between the extant and soil seed bank floras in this study suggests that only a subset of the herbaceous plants surveyed use the seed bank as a mechanism for population maintenance (Hanlon et al. 1998). Furthermore, the potential of soil seed banks, particularly in degraded areas, to act as source of exotic plant invasions may hinder rather than help restoration efforts (Williams et al. 2008; O'Donnell et al. 2014).

Our results indicate that soil seed banks are likely to be least useful in the restoration of wetland *forests* where the dominant plants are woody and clonal. In the absence of large disturbances (i.e. fires or floods, which may provide safe sites for recruitment and trigger the large-scale release of canopy-stored seed and/or promote vegetative reproduction) woody plant propagules may need to be introduced in restoration activities, such as via plantings or direct seeding. Natural regeneration of woody wetland plants is likely to require appropriate water regimes and the presence of mature remnant vegetation as a source of seed (Mahoney and Rood 1998; O'Donnell et al. 2014). Maintaining (or reconnecting) dispersal pathways (e.g. floodplain connectivity) and intact native vegetation upstream may provide other important potential sources of seed for woody plant regeneration (Middleton 2003; O'Donnell et al. 2016). However, in cases where the restoration of woody vegetation is imperative, e.g. for the maintenance of critical habitat for endangered arboreal fauna, target species will often need to be planted or sown (Boudell and Stromberg 2008; O'Donnell et al. 2014).

In wetlands, as in other vegetation communities, complementary mechanisms of regeneration are involved in the maintenance of floristic diversity (Thompson and Grime 1979). Consequently, a mixed approach to the restoration of wetland plant

communities is likely to be most successful (Boudell and Stromberg 2008). Soil seed banks may provide a source of propagules for pioneer vegetation and some perennial herbaceous species, thus facilitating vegetation regeneration (O'Donnell et al. 2016). However, for woody plants, their introduction via direct seeding or planting is likely to be necessary in the short-term, with the preservation of remnant vegetation and maintenance of appropriate water regimes and dispersal pathways important for ensuring the ability of wetland forests to self-sustain in the long-term.

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## Appendix 1

See Table 3.

**Table 3** List of species surveyed across all four sites listed in order of decreasing frequency of occurrence

Scientific name	Origin	Growth form	Life-span	Occurrences	Mean cover (%)
<i>Eucalyptus camphora</i> subsp. <i>humeana</i>	Native	Tree/shrub	p	7	36
<i>Carex appressa</i>	Native	Sedge	p	7	14
<i>Phragmites australis</i>	Native	Grass	p	5	8
<i>Baumea rubiginosa</i>	Native	Sedge	p	4	14
<i>Melaleuca squarrosa</i>	Native	Tree/shrub	p	4	12
<i>Senecio minimus</i>	Native	Forb	a	4	3
<i>Centella cordifolia</i>	Native	Forb	p	4	1
<i>Acacia melanoxylon</i>	Native	Tree/shrub	p	3	10
<i>Tetrarrhena juncea</i>	Native	Grass	p	3	6
<i>Gahnia radula</i>	Native	Sedge	p	3	4
<i>Rubus anglocandicans</i>	Exotic	Tree/shrub	p	3	3
<i>Leptospermum lanigerum</i>	Native	Tree/shrub	p	3	3
<i>Gonocarpus humilis</i>	Native	Forb	p	3	2
<i>Galium aparine</i>	Exotic	Forb	a	3	2
<i>Persicaria praetermissa</i>	Native	Forb	p	3	1
<i>Schoenus lepidosperma</i>	Native	Sedge	p	3	1



**Table 3** continued

Scientific name	Origin	Growth form	Life-span	Occurrences	Mean cover (%)
<i>Austrocynoglossum latifolium</i>	Native	Forb	p	3	1
<i>Prunella vulgaris</i>	Exotic	Forb	p	3	1
<i>Lotus corniculatus</i>	Exotic	Forb	p	3	1
<i>Hypochaeris radicata</i>	Exotic	Forb	p	3	0
<i>Anthoxanthum odoratum</i>	Exotic	Grass	p	2	14
<i>Ranunculus repens</i>	Exotic	Forb	p	2	11
<i>Holcus lanatus</i>	Exotic	Grass	p	2	4
<i>Baloskion tetraphyllum</i>	Native	Restio	p	2	3
<i>Coprosma quadrifida</i>	Native	Tree/shrub	p	2	3
<i>Triglochin procera</i>	Native	Forb	p	2	1
<i>Ranunculus inundatus</i>	Native	Forb	p	2	1
<i>Cardamine hirsuta</i>	Exotic	Forb	a	2	1
<i>Baumea tetragona</i>	Native	Sedge	p	1	2
<i>Lomandra longifolia</i>	Native	Rush	p	1	2
<i>Melaleuca ericifolia</i>	Native	Tree/shrub	p	1	2
<i>Leptospermum scoparium</i>	Native	Tree/shrub	p	1	1
<i>Banksia marginata</i>	Native	Tree/shrub	p	1	1
<i>Pteridium esculentum</i>	Native	Fern	p	1	1
<i>Potentilla indica</i>	Exotic	Forb	p	1	1
<i>Poa annua</i>	Exotic	Grass	a	1	1
<i>Dianella tasmanica</i>	Native	Xan	p	1	1
<i>Xanthorrhoea minor</i>	Native	Xan	p	1	1
<i>Cirsium vulgare</i>	Exotic	Forb	a	1	1
<i>Persicaria subsessilis</i>	Native	Forb	p	1	1
<i>Poa tenera</i>	Native	Grass	p	1	1
<i>Callitriche stagnalis</i>	Exotic	Forb	a/p	1	<1
<i>Isolepis inundata</i>	Native	Sedge	p	1	<1
<i>Juncus procerus</i>	Native	Rush	p	1	<1
<i>Austrostipa</i> sp.	Native	Grass	p	1	<1
<i>Solanum nigrum</i>	Exotic	Forb	a	1	<1
<i>Acaena novae-zelandiae</i>	Native	Forb	p	1	<1
<i>Juncus sarophorus</i>	Native	Rush	p	1	<1
<i>Lobelia anceps</i>	Native	Forb	p	1	<1
<i>Rumex conglomeratus</i>	Exotic	Forb	a	1	<1
<i>Mentha australis</i>	Native	Forb	p	1	<1
<i>Lomandra filiformis</i>	Native	Rush	p	1	<1
<i>Euchiton involucratus</i>	Native	Forb	a	1	<1
<i>Juncus prismatocarpus</i>	Native	Rush	p	1	<1
<i>Trifolium repens</i>	Exotic	Forb	p	1	<1
<i>Hypochaeris glabra</i>	Exotic	Forb	a	1	<1
<i>Urtica urens</i>	Exotic	Forb	a	1	<1

Species characteristics presented: origin (native or exotic); growth form (rush, sedge, grass, forb, tree/shrub), and life-span (a—annual/biennial; p—perennial). Occurrences = no. of quadrats (out of eight) in which that species was observed. Mean cover = average cover of that species across all surveyed quadrats

## Appendix 2

See Table 4.

**Table 4** List of seed bank taxa listed in order of decreasing density

Scientific name	Origin	Growth form	Life-span	Total nos. of seedlings	Mean density (seedlings/m <sup>2</sup> )
<i>Juncus bufonius</i>	Native	Rush	a	963	2452.26
<i>Juncus bulbosus</i>	Exotic	Rush	p	742	1889.49
<i>Juncus articulatus</i>	Exotic	Rush	p	666	1695.96
<i>Juncus planifolius</i>	Native	Rush	a	647	1647.57
<i>Isolepis inundata</i>	Native	Sedge	p	523	1331.81
<i>Juncus procerus</i>	Native	Rush	p	492	1252.87
<i>Senecio minimus</i>	Native	Forb	a	418	1064.43
<i>Gratiola pubescens</i>	Native	Forb	p	287	730.84
<i>Carex appressa</i>	Native	Sedge	p	211	537.31
<i>Cardamine hirsuta</i>	Exotic	Forb	a	149	379.43
<i>Ranunculus repens</i>	Exotic	Forb	p	143	364.15
<i>Lobelia anceps</i>	Native	Forb	p	122	310.67
<i>Anthoxanthum odoratum</i>	Exotic	Grass	p	121	308.12
<i>Baloskion tetraphyllum</i>	Native	Rush	p	117	297.94
<i>Holcus lanatus</i>	Exotic	Grass	p	98	249.55
<i>Centella cordifolia</i>	Native	Forb	p	80	203.72
<i>Austrocynoglossum latifolium</i>	Native	Forb	p	45	114.59
<i>Centrolepis fascicularis</i>	Native	Sedge	p	43	109.50
<i>Lotus corniculatus</i>	Exotic	Forb	p	43	109.50
<i>Callitriche stagnalis</i>	Exotic	Forb	a	41	104.41
Unknown grass sp. 1	Unknown	Grass		36	91.67
<i>Juncus capitatus</i>	Exotic	Rush	a	33	84.03
<i>Lolium perenne</i>	Exotic	Grass	p	33	84.03
<i>Solanum nigrum</i>	Exotic	Forb	a	30	76.39
<i>Isolepis levynsiana</i>	Exotic	Sedge	a	20	50.93
<i>Sisyrinchium iridifolium</i>	Exotic	Forb	a	19	48.38
<i>Gonocarpus micranthus</i>	Native	Forb	p	18	45.84
<i>Stellaria media</i>	Exotic	Forb	a	18	45.84
<i>Trifolium dubium</i>	Exotic	Forb	a	16	40.74
<i>Cirsium vulgare</i>	Exotic	Forb	a	15	38.20
<i>Hypericum gramineum</i>	Native	Forb	p	14	35.65
<i>Phalaris arundinacea</i>	Exotic	Grass	p	12	30.56
<i>Juncus prismatocarpus</i>	Native	Rush	p	11	28.01
<i>Kunzea ericoides</i>	Native	Tree/shrub	p	10	25.46
<i>Cardamine tenuifolia</i>	Native	Forb	p	9	22.92
<i>Centaureum tenuiflorum</i>	Exotic	Forb	a	7	17.83
<i>Leptospermum lanigerum</i>	Native	Tree/shrub	p	6	15.28
<i>Rubus anglocandicans</i>	Exotic	Tree/shrub	p	6	15.28
<i>Typha latifolia</i>	Exotic	Typha	p	6	15.28
<i>Cerastium glomeratum</i>	Exotic	Forb	a	5	12.73

**Table 4** continued

Scientific name	Origin	Growth form	Life-span	Total nos. of seedlings	Mean density (seedlings/m <sup>2</sup> )
<i>Hypochaeris radicata</i>	Exotic	Forb	p	5	12.73
<i>Myriophyllum pedunculatum</i>	Native	Forb	p	5	12.73
<i>Poa tenera</i>	Native	Grass	p	5	12.73
<i>Acacia melanoxylon</i>	Native	Tree/shrub	p	4	10.19
<i>Banksia spinulosa</i>	Native	Tree/shrub	p	4	10.19
<i>Eleocharis gracilis</i>	Native	Sedge	p	4	10.19
<i>Eragrostis brownii</i>	Native	Grass	p	4	10.19
<i>Euchiton involucratus</i>	Native	Forb	a	4	10.19
<i>Gonocarpus humilis</i>	Native	Forb	p	4	10.19
<i>Lomandra filiformis</i>	Native	Rush	p	4	10.19
<i>Lotus uliginosus</i>	Exotic	Forb	p	4	10.19
<i>Lycopus australis</i>	Native	Forb	p	4	10.19
<i>Trifolium glomeratum</i>	Exotic	Forb	a	4	10.19
<i>Urtica urens</i>	Exotic	Forb	a	4	10.19
<i>Isolepis cernua</i>	Native	Sedge	p	3	7.64
<i>Ranunculus amphitrichus</i>	Native	Forb	p	3	7.64
<i>Ranunculus flammula</i>	Exotic	Forb	p	3	7.64
<i>Rumex conglomeratus</i>	Exotic	Forb	a	3	7.64
<i>Acaena novae-zelandiae</i>	Native	Forb	p	2	5.09
<i>Baumea tetragona</i>	Native	Sedge	p	2	5.09
<i>Casinia arcuata</i>	Native	Tree/shrub	p	2	5.09
<i>Centripeda cunninghamii</i>	Native	Forb	p	2	5.09
<i>Centrolepis strigosa</i>	Native	Sedge	a	2	5.09
<i>Dianella tasmanica</i>	Native	Xan	p	2	5.09
Unknown grass sp. 2	Unknown	Grass		2	5.09
<i>Galium aparine</i>	Exotic	Forb	a	2	5.09
<i>Helichrysum luteoalbum</i>	Native	Forb	a	2	5.09
<i>Hydrocotyle pterocarpa</i>	Native	Forb	p	2	5.09
<i>Ozothamnus ferrugineus</i>	Native	Tree/shrub	p	2	5.09
<i>Prunella vulgaris</i>	Exotic	Forb	p	2	5.09
<i>Sagina procumbens</i>	Exotic	Forb	p	2	5.09
<i>Sonchus oleraceus</i>	Exotic	Forb	a	2	5.09
<i>Trifolium repens</i>	Exotic	Forb	p	2	5.09
<i>Caesia parviflora</i>	Native	Sedge	p	1	2.55
<i>Carex fascicularis</i>	Native	Sedge	p	1	2.55
<i>Centrolepis aristrata</i>	Native	Sedge	a	1	2.55
<i>Conyza bonariensis</i>	Exotic	Forb	a	1	2.55
<i>Drosera peltata</i>	Native	Forb	p	1	2.55
<i>Gratiola peruviana</i>	Native	Forb	p	1	2.55
<i>Lepyrodia muelleri</i>	Native	Forb	p	1	2.55

Taxa characteristics presented: origin (native or exotic); growth form (rush, sedge, grass, forb, tree/shrub), and life-span (a—annual/biennial; p—perennial). Total nos. of seedlings = total numbers of seedlings of that taxa that emerged from all collected samples (n = 40). Mean density = the average density of seedlings/m<sup>2</sup> of topsoil (top 5 cm of soil) for that taxa across all samples collected

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