

Resilience of soil seed banks to site degradation in intermittently flooded riverine woodlands

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Abstract

Questions: (1) What is the recovery potential of soil seed banks of intact, average and degraded floodplain woodlands? (2) Will soil seed banks of different functional groups (native and exotic, dryland and wetland) display contrasting responses to site degradation?

Location: Semi-arid, seasonally flooded woodland of eastern Australia.

Methods: Diversity, abundance and composition of soil seed banks were assessed using a glasshouse study. Surface soil samples were taken from a total of nine sites with three levels of degradation (intact, average, degraded) from three microsites (sub-canopy, canopy edge, open).

Results: A total of 26 662 individuals of 82 species germinated. Seed abundance increased tenfold from intact to degraded sites, but there was no effect on richness. Species composition of all functional groups varied significantly among degradation states. Seeds of native wetland and exotic dryland species were more abundant in degraded than in intact sites. However, the abundance of native dryland germinants did not differ among degradation classes and no seeds of exotic wetland species were observed. Richness of exotic dryland species was significantly higher in degraded sites.

Conclusions: Increasing disturbance promoted seed banks of exotic but not native dryland species and native but not exotic wetland species. Unexpectedly, disturbance promoted the abundance of native seeds more than exotics, although this was driven by a single species. Our results suggest that the dryland

phase of the floodplain community is more resilient to degradation than predicted.

Key words: Ecosystem resilience; Floodplain vegetation; Germinable seed; Invasive plants; Wetlands.

Nomenclature: Harden (1992–2002).

Introduction

Globally, riverine floodplain habitats are subject to intensive human land use. Remnant vegetation is often highly fragmented, degraded and susceptible to human disturbances, such as livestock grazing, agriculture, soil disturbance, timber harvesting and altered flooding regimes (Tockner & Stanford 2002; Dudgeon et al. 2006). Consequently, understanding the resilience (*sensu* Westman 1986) or recovery potential of degraded floodplain remnants is critically important for conservation management.

The ability to recover following removal of degrading processes varies greatly among species within any particular habitat as a consequence of differing capacities to recruit, persist, grow, breed and/or disperse into disturbed or degraded areas (Elmqvist et al. 2003). Persistent soil seed banks confer resilience on many species by enabling populations to persist through, and recover from, adverse environmental conditions, particularly in temporally unpredictable habitats (Grime 1979; Pake & Venable 1996). Wetland plants commonly possess large persistent soil seed banks, especially in environments where flooding and drying cycles are unpredictable (Brock et al. 2003). While moist soils promote rapid germination and establishment, some seeds persist across flooding cycles, buffering populations against adverse conditions such as deep flooding or rapid drying (Brock et al. 2003). Persistent seed banks and buried bud banks provide a high degree of resilience to many intermittent and seasonal wetlands, allowing some plant species to persist not only through adverse weather conditions, but also through human disturbances, such as soil disturbance and irrigated agriculture (McIntyre 1985).

In contrast to wetland habitats, temperate grasslands and grassy woodlands are often highly

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susceptible to degradation from anthropogenic disturbances such as farming and livestock grazing, especially in regions where native vegetation did not evolve under heavy ungulate grazing (Mack 1989; Lunt et al. 2007). In these areas, perennial native species commonly possess small or short-lived soil seed banks, which are dominated by short-lived exotic species (Lunt 1990; Gilfedder & Kirkpatrick 1993; Morgan 1998; Lodge 2001), thereby conferring little resilience following degradation of the standing vegetation. This is exemplified in temperate grasslands and grassy woodlands of southern Australia, where soil seed banks are dominated by exotic species, and many native species persist through a “bud bank” rather than a persistent soil seed bank (Lunt & Morgan 2002).

Floodplain habitats possess a combination of wetland and dryland species, which alternate in abundance during wetting and drying phases of flood cycles. By extension from soil seed bank patterns documented in spatially discrete wetland and dryland habitats, seed banks of co-occurring wetland and dryland species in floodplain habitats may be expected to display contrasting responses to human-induced ecosystem degradation. Thus, the soil seed bank of a degraded floodplain woodland may be predicted to be dominated by a suite of native wetland species (since native wetland species commonly form large seed banks in intermittent wetlands to permit survival during unfavourable conditions; Brock et al. 2003) and a second suite of exotic terrestrial species, with relatively few seeds of exotic wetland or native terrestrial species (Pettit & Froend 2001; Robertson & James 2007; Williams et al. 2008). Unless moderated by differential patterns of resprouting or dispersal, such a pattern would result in alternating phases of dominance by exotic and native species during dry and wet periods, respectively. Consequently, estimates of site condition, resilience or site degradation status gathered during dry periods may greatly underestimate site condition during wet phases.

The Murrumbidgee Irrigation Area (MIA) is a large (6000 km²) productive, agricultural region on the Murrumbidgee River in the Murray-Darling Catchment in southeastern Australia. The original floodplain ecosystems, including *Eucalyptus camaldulensis* Dehnh. (River Red Gum) and *E. largiflorens* F. Muell. (Black Box) woodlands, have been subject to spatially and temporally variable flooding regimes, and possess a mixture of species typical of terrestrial dryland habitats and intermittent wetlands (Alexander et al. 2008). Most remnants are now highly degraded and many are

isolated by irrigated agriculture. Considerable efforts are being devoted to conserving and restoring degraded remnants, including removal of livestock and provision of environmental flows to restore natural flooding regimes (Alexander et al. 2008). However, while considerable attention has been given to ecosystem function and resilience in wetland communities, relatively little is known of the factors that influence ecological resilience in degraded riverine woodlands (e.g. Robertson & James 2007; Williams et al. 2008).

In this study we compare soil seed bank composition between intact and degraded floodplain woodlands dominated by *E. largiflorens* in the MIA. We hypothesized that the soil seed banks of native and exotic species and of dryland and wetland species would display contrasting responses, particularly to site degradation. First, among the dryland component of the floodplain seedbank, we predicted that (1) the soil seed bank would be dominated by exotic species with relatively few seeds of native plants, and (2) with increasing site degradation, seeds of exotic dryland species would become more abundant, and the abundance and richness of native dryland species would decline. Second, among the wetland component of the floodplain seed bank (3) seeds of native species would be more abundant than those of exotic species, and (4) increasing site degradation would have little effect on the abundance and richness of seeds of wetland species. We examined these four hypotheses in a seed bank study across sites varying from degraded through to intact, in remnant floodplain woodlands in the MIA.

Methodology

Field sampling

The study was conducted at nine remnant *E. largiflorens* woodlands (sites) within 20 km of Griffith in southwestern New South Wales, Australia (34°05′-34°35′E, 145°35′-146°08′S). Sites were selected based on a regional assessment of remnant vegetation (Eldridge et al. 2007). Soils are usually medium to heavy grey cracking clays (Vertisols), sometimes overlain by clay loams and loams. Slopes are generally <1%, with little evidence of erosion. The area is semi-arid and experiences a typical Mediterranean climate, characterized by hot, dry summers averaging 15-31°C and cool winters (3-15°C). Annual rainfall averages about 300 mm, and about 25% of rain falls in the cooler months (Department of Primary Industries, Griffith).

Remnant woodlands would have received natural flood water on average about once every decade, but many have not received flood water for more than 20 years.

The density of *E. largiflorens* among sites ranged from 10 to 400 trees · ha⁻¹ (mean = 117 trees · ha⁻¹). Tree health, as assessed by the degree of canopy dieback, ranged from excellent to poor, with a mean score of ca. 75% of full canopy growth. Shrub cover was generally very sparse, although sites in good health usually supported a moderate to dense cover of *Rhagodia spinescens*, and regularly inundated sites contained varying densities of *Muehlenbeckia florulenta*. *R. spinescens* is a moderately long-lived, grazing-intolerant perennial sub-shrub up to 1.5-m high. *M. florulenta* is a long-lived, drought-tolerant perennial shrub that is a common component of intermittently flooded wetlands. Both shrub species have high habitat and grazing value, and are indicative of well-managed intact sites. Sites were dry when sampled, and ground vegetation was dominated by exotic (mostly annual) grasses and forbs (*Hordeum leporinum*, *Bromus cartharticus*, *B. diandrus*, *Lolium* spp., *Sisymbrium* spp., *Echium plantagineum*, *Marrubium vulgare*), and the native species *Einadia nutans* ssp. *nutans*, *Austroanthonia caespitosa*, *Austrostipa scabra* and *Marsilea drummondii*. Plant nomenclature follows Harden (1992–2002).

Site degradation was ranked on a 10-point scale from highly degraded (rating = 1) to intact (rating = 10). Prior research demonstrated that degradation rankings were highly correlated ($F_{1,18} = 38.5$ $R^2 = 0.68$, $P < 0.001$) with independent measures of site condition derived from 25 biotic and abiotic attributes, ranging from cover and composition of the vascular vegetation, to degree of erosion and soil fertility (Eldridge et al. 2007).

Nine sites were randomly selected across the study area (~400 km²) based on their condition in order to span a range of degradation states from degraded (mean score = 4.8), through average (7.5) to intact (8.8). Degraded sites had significantly lower values for landscape structure and composition, vegetation patchiness (i.e. the arrangement of grass butts and logs on the surface), cover of vascular and non-vascular plants and leaf litter, and richness of native vascular plants (Table 1). By contrast, intact sites had greater landscape patchiness, with more micro-surface obstructions, such as grass butts and logs. Cover of exotic plants increased with site degradation, and was particularly high in degraded sites (Table 1, Eldridge et al. 2007).

At each site, four replicate locations (Blocks) were selected, each centering on a mature *E. largi-*

Table 1. Description of the three degradation states derived from detailed field survey (Eldridge et al. 2007); #Indicates subjective assessment given to sites based on expert knowledge, where 10 is intact and 1 is extremely poor. For each attribute, different subscripts indicate significant differences between degradation states at $P < 0.05$.

Attribute	Intact		Average		Degraded	
	Mean	SEM	Mean	SEM	Mean	SEM
Groundstorey richness	26.7 ^a	3.8	22.3 ^a	4.4	18.4 ^a	0.7
Native species richness	16.4 ^a	2.3	16.0 ^a	2.3	5.3 ^b	0.9
Exotic species richness	10.3 ^a	1.5	6.3 ^a	2.1	13.1 ^a	1.6
Groundstorey cover (%)	45.0 ^a	2.9	43.3 ^a	18.3	45.0 ^a	16.1
Native plant cover (%)	27.7 ^a	1.8	32.9 ^a	15.5	11.4 ^a	3.3
Exotic plant cover (%)	17.3 ^a	1.1	10.4 ^a	2.8	33.6 ^b	12.9
Cryptogam cover (%)	10.0 ^a	10.0	5.3 ^a	5.3	0 ^a	0
Grass basal cover (%)	2.0 ^a	1.1	0.3 ^a	0.27	0 ^a	0
Tree cover (%)	13.0 ^a	2.0	16.0 ^a	10.4	15.0 ^a	5.0
Landscape structure (%)	63.2 ^a	3.86	48.6 ^b	4.23	47.9 ^b	0
Landscape composition (%)	66.7 ^a	2.40	63.9 ^a	1.40	43.0 ^b	2.77
Landscape function (%)	75.5 ^a	3.55	69.6 ^a	4.27	71.6 ^a	0.97
Soil organic carbon (%)	6.7 ^a	0.53	5.5 ^a	2.74	3.4 ^a	0.70
Ecosystem condition score [#]	8.8 ^a	0.0	7.5 ^a	0.29	4.8 ^b	0.44

florens tree. The distance between each of the four trees at a given site ranged from 300–600 m; thus the trees were considered to be statistically independent in terms of the vegetation and soil seed banks. Soils were collected from three microsites at each location: (1) under the tree canopy (“canopy microsite”), (2) at the edge of the canopy (“edge”) and (3) approximately 20 m away from any canopy (“open”). Patches of bare soil more than 30-cm diameter were avoided. Trees are known to be focal points of plant cover and composition in semi-arid woodlands (Warnock et al. 2007). Consequently, we sampled the three microsites to accommodate marked spatial patterning of understory plants in relation to canopy trees, and to determine whether degradation had different effects on soil seed banks in contrasting microsites. At each microsite, three samples were collected, each of 10 cm × 15-cm area (0.015 m²), 20-mm depth and ca. 500-g weight. Samples were bulked and mixed, and a 1 kg subsample was taken back to the glasshouse. In total, 108 samples were collected (three degradation classes × three sites × four locations × three microsites).

Seed germination

Seed bank composition was examined using the seedling emergence method. Approximately 300 g of soil from each microsite were spread over propagating sand in shallow germination trays (345 × 285 × 55 mm). Control trays containing propagating sand only were used to identify glasshouse

weeds. In January 2003, trays were placed in a random design in a naturally heated glasshouse. Average air temperature ranged from 17.3°C to 24.2°C. An automatic sprinkler system watered trays twice daily. By June 2003 few germinants were observed so trays were allowed to dry out and were placed in a cool room (4°C) to simulate winter conditions, until mid-August when they were returned to the glasshouse. The germination trial then continued until late November. Seedlings were regularly identified, counted and removed from trays. Those that could not be identified were transplanted and grown in larger pots.

Statistical analyses

Differences in seedling abundance and species richness were explored in relation to degradation status and microsite (and their interactions) using ANOVA (Minitab 2007) after checking for homogeneity of variances using Levene's test, and running diagnostic tests within the Minitab package. The ANOVA model was a mixed model with three error terms (Table 2). The first stratum considered degradation status; the second stratum, which comprised only an error term with 27 df, accounted for variance between individual trees at a site; and the third stratum considered microsite and its interaction with degradation status. Significant differences in means between degradation classes were compared using Tukey's least significant difference (LSD) tests.

Composition of the germinable seedbank was examined in relation to degradation status and microsites using a matrix of 82 columns (species) by 108 rows (sites, locations and microsites). We used permutational multivariate analysis of variance (PERMANOVA, Anderson et al. 2008) to test whether plant composition varied among degradation states, microsites and their interactions. PERMANOVA allowed us to partition the multivariate

variation using the structure described above for the univariate analyses. Two matrices, one of plant abundance [$\log(10)$ -transformed] and the other presence-absence data, were converted to similarity matrices using the Bray Curtis similarity coefficients contained within the PRIMER-E statistical package. Pair-wise *a posteriori* comparisons were made, where necessary, using a multivariate analogue of the *t*-statistic, the probability levels being obtained by permutation.

The degree of association of individual species with degradation states and microsites was measured using indicator-species analysis (Dufrene & Legendre 1997). Indicator values (IV) combine information on relative abundance and species frequency. Values are maximal (IV = 100) when all individuals of a given species are restricted to a particular degradation class and all samples from that degradation class contain the species. Indicator value analysis was performed using PC-ORD (McCune & Mefford 1999). Species data were randomized among degradation classes and microsites, and a Monte-Carlo randomization procedure was performed with 1000 iterations to determine the statistical significance of the indicator values.

To examine relationships between plant functional groups and site degradation state, we classified species according to their habitat (Wetland, Dryland, Mixed), origin (Native, Exotic) and Life form (Annual, Perennial) using regional and local floras (Cunningham et al. 1981). No analyses were performed on the Mixed habitat group, and we did not observe any exotic wetland plants. For each group, we used separate one-way ANOVAs on $\log(10)$ or \sin^{-1} transformed data (Minitab 2007) to examine responses in relation to the three levels of site degradation (intact, average, degraded) using richness (number of species) and abundance (number of individuals) data averaged across replicates and microsites. Permutational multivariate analysis of variance was again used to examine effects of site degradation and microsite (and their interaction) on the composition of each functional group (WN, DE, DN) using both abundance and presence-absence data separately.

Table 2. ANOVA structure for analysis of total species abundance.

Source	DF	SS	MS	F	P
Site × condition stratum					
Condition	2	16.575	8.287	6.70	0.030
Residual	6	7.421	1.237	14.22	
Site × condition × set stratum	27	2.348	0.087	1.17	0.297
Site × condition × set × microsite stratum					
Microsite	2	1.224	0.612	8.23	0.001
Condition × microsite	4	0.384	0.096	1.29	0.282
Residual	66	4.908	0.074		
Total	107	32.860			

Results

Eighty-two species (26 662 individuals, 26 333 seeds m^{-2}) were recorded from the soil seed bank, of which 12 (19 610 individuals) were wetland species (all native). Of the 47 dryland species recorded (6146 individuals), there were similar

numbers of native (23) and exotic (24) species (Hypothesis 1). Twenty-three species were categorized as either wetland or dryland (seven exotic, 16 native, 906 individuals), but no exotic wetland plants were recorded (Hypothesis 3). The native sedge *Cyperus difformis* accounted for 66% of all germinants.

Degradation effects on the entire seed bank

Increasing site degradation was associated with a significant increase in germinant abundance, from 5212 ± 590 germinants m^{-2} in intact sites to 54614 ± 7520 (mean \pm SEM) \cdot germinants $\cdot m^{-2}$ in degraded sites ($F_{2,6} = 6.70$, $P = 0.030$ on log(10)-transformed data). This trend was also consistent when we removed the dominant species *C. difformis* ($F_{2,6} = 5.56$, $P = 0.043$ on square-root-transformed data). In contrast to trends in germinant abundance, site degradation status had no significant effect on species richness, with only slightly more species per sample (15.7) in degraded compared with intact sites (10.9 species; $P > 0.05$; Table 3).

Species composition of the soil seed bank (using abundance data) varied significantly among all three degradation states (pseudo $F_{2,6} = 3.65$, P (perm) = 0.046), although there was a high degree of overlap in the composition of average and intact sites. Indicators of degraded sites included the dryland exotic *E. plantagineum* (IV = 65.3, $P < 0.001$), the dryland native *Eriochloa australiensis* (IV = 60.2, $P < 0.001$) and the wetland natives, *C. difformis* (IV = 75.4, $P < 0.001$), *Eragrostis parviflora* (IV = 53.3, $P < 0.001$) and *Lythrum hyssopifolium* (IV = 41.7, $P = 0.007$). The dryland native species *Crasula colorata* var. *acuminata* (IV = 58.4, $P < 0.001$) and *E. nutans* (IV = 57%, $P < 0.001$), and the wetland native *Amphibromus fluitans* (IV = 47.7, $P = 0.002$) were significant indicators of average sites. The best indicators of intact sites were the dryland exotic herb *Spergularia rubra* (IV = 37.7, $P < 0.001$) and dryland native grass *Austrodanthonia setacea* (IV = 32.4, $P < 0.001$). Trends were very si-

milar when either presence-absence or abundance data were used.

Microsite effects on the entire seed bank

Seed abundance was lower under the canopy (20 308 seeds m^{-2}) than at the canopy edge (28 332 seeds m^{-2}) or in open microsites (30 359 seeds m^{-2} ; $F_{2,66} = 8.23$, $P = 0.001$ on log(10)-transformed data). Fewer species were also found in each sample at the canopy sites (11.4 species) than in either the open (13.3) or edge (13.8) microsites ($F_{2,66} = 4.59$, $P = 0.014$), and there were no significant degradation by microsite interactions for either abundance or richness ($P > 0.05$). The composition at canopy microsites was also significantly different to that at the other microsites (pseudo $F_{2,66} = 4.09$, P (perm) = 0.001). *Sisymbrium erysimoides* was strongly associated with canopy microsites (IV = 75.9%, $P = 0.03$) but no species were indicative of open or canopy edge microsites ($P > 0.05$).

Degradation status and plant functional groups

Contrary to prediction (Hypothesis 4), germinants of native wetland species became significantly more abundant with declining degradation status ($F_{2,6} = 5.3$, $P = 0.04$), and were 24-times more abundant in degraded than in intact sites (Fig. 1). This pattern was due to *C. difformis*, which accounted for 89% of all native wetland germinants (Table 3). Consequently, there was no significant difference in the abundance of native wetland species between the three degradation classes when *C. difformis* was excluded from the analysis ($P = 0.50$; Table 3). Germinants of native dryland species were 2-3-times more abundant in average sites than the other degradation classes, but the differences were not significant (Hypothesis 2: $P = 0.13$; Fig. 1). By contrast, exotic dryland germinants (Hypothesis 2) were 6-14-times more abundant in degraded than average or intact sites ($F_{2,6} = 7.95$, $P = 0.021$;

Table 3. Average species abundance (seedlings m^{-2}) and richness (species per tray) of seeds of contrasting plant functional groups in three degradation states in floodplain woodlands. For a given attribute and functional group, different subscripts indicate significant differences at $P < 0.05$. #Richness significant at $P = 0.068$.

Functional group	Germinant abundance			Species richness		
	Intact	Average	Degraded	Intact	Average	Degraded
All species [#]	5212 ^a	19173 ^b	54614 ^b	10.9 ^a	12.1 ^a	15.7 ^a
<i>Cyperus difformis</i>	806 ^a	11947 ^{ab}	39043 ^b	0.9 ^a	1.0 ^a	1.0 ^a
All species except <i>C. difformis</i>	4406 ^a	7227 ^{ab}	15570 ^b	10.0 ^a	11.1 ^a	14.7 ^a
Native wetland, except <i>C. difformis</i>	945 ^a	2311 ^a	3052 ^a	1.8 ^a	2.6 ^a	1.9 ^a

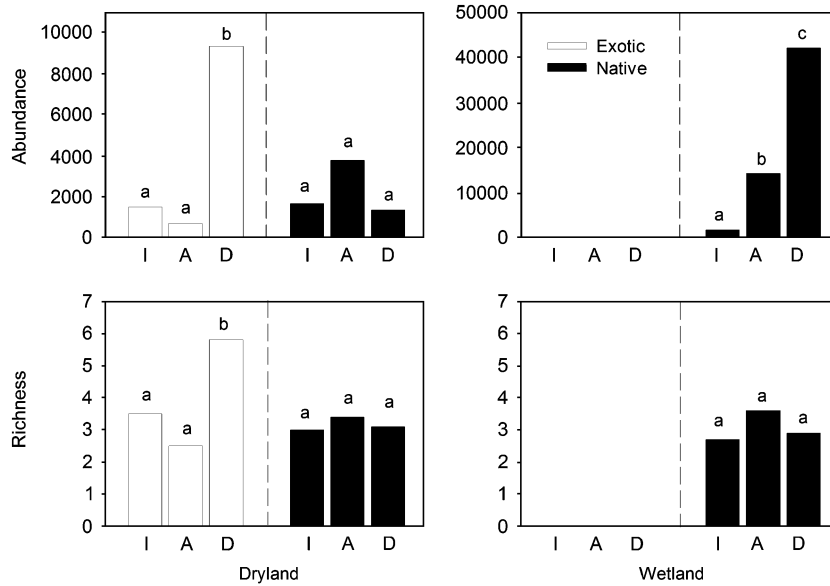


Fig. 1. Abundance (seedlings m⁻²) and richness (species per tray) of native and exotic dryland and wetland seeds. Different letters within a native or exotic group indicate a significant difference in abundance or richness among degradation states at $P < 0.05$. I = intact, A = average, D = degraded.

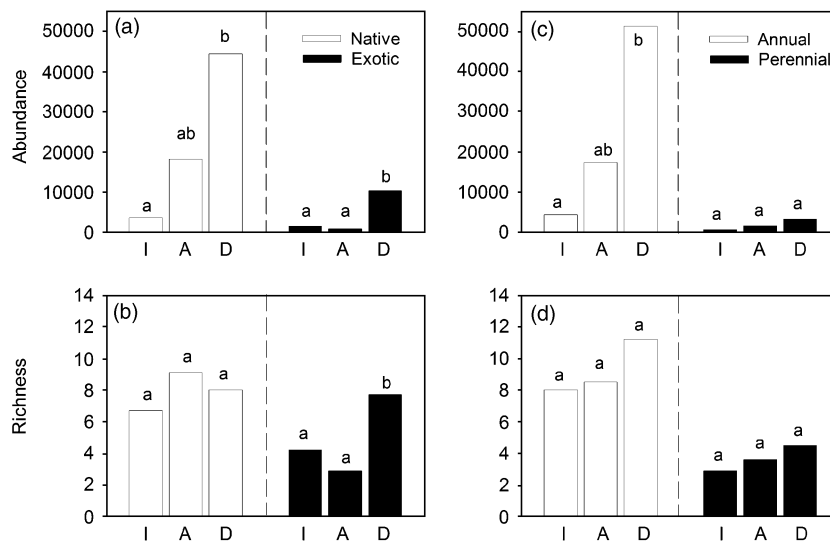


Fig. 2. Abundance (seedlings m⁻²) and richness (species per tray) of (a) total native and (b) total exotic seeds, and (c) total annual and (d) total perennial seeds. Different letters among a cluster of degradation states indicate a significant difference in abundance or richness at $P < 0.05$. I = intact, A = average, D = degraded.

Fig. 1). Germinants of annual species were almost 12-times more abundant in degraded than intact sites ($P = 0.006$), but perennial species did not differ significantly across degradation states ($P = 0.374$; Fig. 2).

In general, species richness of each functional group was relatively similar across the degradation gradient, although there were significantly more

exotic dryland species per sample in degraded sites (5.8 species) than in intact (3.5 species) or average (2.5 species) sites ($F_{2,6} = 19.13$, $P = 0.002$), but no difference in native dryland species (3.1-4.3 species, $P = 0.08$; Hypothesis 2; Fig. 1).

Differences in species composition among degradation classes were more apparent when abundance data, rather than presence-absence data,

were analysed. Based on abundance data, using $\log(10) x+1$ transformations, the composition of both native dryland (pseudo $F_{2,6} = 3.20$, P (perm) = 0.009) and exotic dryland (pseudo $F_{2,6} = 2.87$, P (perm) = 0.006) species differed significantly among all three degradation classes. Composition of native wetland was marginally different between the intact and degraded sites only (pseudo $F_{2,6} = 3.62$, P (perm) = 0.074).

Based on presence-absence data, the composition of native dryland species differed significantly among all degradation classes (pseudo $F_{2,6} = 4.12$, P (perm) = 0.003), while exotic dryland species only differed significantly between the degraded class and the other classes (pseudo $F_{2,6} = 3.53$, P (perm) = 0.006). For the wetland natives, however, there were no significant differences in composition among degradation classes (P (perm) = 0.490).

In general, we detected significant differences between canopy microsites and other microsites for native dryland (pseudo $F_{2,66} = 5.59$, P (perm) = 0.001) and native wetland (pseudo $F_{2,66} = 4.00$, P (perm) = 0.001) species, and differences between all microsites for exotic dryland species (pseudo $F_{2,66} = 3.58$, P (perm) = 0.001) when using abundance data. Trends were very similar using presence-absence data except, that for exotic dryland species, only the canopy microsites differed in their species composition from the other microsites (pseudo $F_{2,66} = 4.64$, P (perm) = 0.001), with *Sisymbrium erysimoides* being indicative of canopy sites.

Discussion

Our results support the hypothesis that soil seed banks of native and exotic species, and dryland and wetland species, display contrasting responses to site degradation in intermittently flooded woodlands. Increasing disturbance enhanced the abundance of exotic seed banks but not of native dryland species and native but not exotic wetland species, although exotic wetland species were totally absent from the system. The total absence of exotic wetland species in the soil seed bank is consistent with other studies that have found that relatively few exotic species have invaded seed banks of wetlands and intermittently flooded areas in Australia (McIntyre et al. 1988). The high resilience of intermittent and seasonal wetland habitats to exotic invasion may be due to strong selection against establishment of new species in this spatially patchy and temporally variable and unpredictable environment, which encompasses hot dry summers as well as lengthy flooding.

Contrary to expectations, disturbance promoted the abundance of native seeds more than exotics, and this pattern was driven by a single species, the small, fast-growing annual sedge *C. difformis*. *C. difformis* accounted for 66% of germinable seeds and 71% of seeds in degraded sites, although it was never observed in the standing vegetation (Eldridge et al. 2007). Seed bank densities of up to 303 000 seeds \cdot m⁻² have been reported on irrigated rice bays close to our sites (McIntyre 1985); such densities greatly exceed those from our study (mean = 2948, max = 205 974 seeds \cdot m⁻² in a degraded canopy microsite). The high densities of *C. difformis* seeds in degraded sites in our study were not related to flooding regimes, which were similar across all degradation classes. Rather, densities probably reflect the high levels of soil disturbance due to historic overgrazing (Sanders 1994; Navie et al. 1996), which has been shown to boost reproductive output of the related *Cyperus sanguinolentus* Vahl. (Crossle & Brock 2002).

Dryland seed banks across disturbance gradients

We also predicted that seed banks would provide less resilience to the dryland phase of the system compared to the wetland phase, since degradation was predicted to promote seeds of exotic dryland species and deplete seeds of native dryland species, while having relatively little impact on the seed banks of wetland species. This hypothesis was partly supported, but our results suggest that the dryland phase is more resilient to degradation than we predicted, since seeds of native dryland species were similarly abundant in intact and degraded sites, and degradation did not promote seeds of exotic dryland species to the marked extent that was predicted. The absence of significant interactions between site degradation and microsites indicated that degradation had similar impacts on seed abundance and richness in all microsites, even though the species contributing to these patterns varied among microsites.

Anthropogenic disturbances are known to promote Mediterranean annual species across temperate Australia (Moore 1973; Mack 1989). However, while exotic annuals are commonly recorded in soil seed bank studies (e.g. Lunt 1990; Morgan 1998; Lodge 2001), few Australian studies have compared seed densities of exotic annuals across degradation or disturbance gradients (Navie et al. 1996; Standish et al. 2007). In our study, seeds of exotic annuals were six times as abundant in degraded as in intact sites. Functionally, this difference

may not affect the abundance of exotic annuals in the standing vegetation, given that seed densities were high in intact sites ($1470 \cdot \text{seeds} \cdot \text{m}^{-2}$) and annual plants can greatly increase levels of seed production in favourable microsites and seasons.

Contrary to our hypotheses, however, there were no significant effects of degradation on abundance or richness of seeds of native dryland species. This result was unexpected, since native species richness and cover were markedly lower in degraded than in average or intact sites in the standing vegetation, although this trend was only significant for richness (Table 1). However, the species composition of native dryland species differed significantly among all three degradation states, even when presence-absence data were analysed. This demonstrates that degradation affected native dryland seed banks, even though seed densities and richness remained relatively constant.

Indicator species analysis showed that intact sites were characterized by the perennial tussock-grass *A. setacea*, average sites by the small annual forb *Crassula colorata*, and degraded sites by the annual summer-growing grass *E. australiensis*. This trend illustrates a change from perennial to annual life forms amongst characteristic indicator species, although this life form change was not apparent when all native dryland species were examined (results not shown, $P > 0.05$). The decline in seed density of *A. setacea* with increasing degradation may have resulted from competition from exotic annuals, as reported elsewhere (Lenz & Facelli 2005; Prober et al. 2005).

Finally, the results of our study support the widespread finding of higher seed densities in disturbed and early-successional habitats compared to undisturbed and late-successional habitats (Grime 1979; Roberts & Vankat 1991; Bossuyt & Hermy 2001). Our hypotheses integrate aspects of Grime's (1974, 1979) C-S-R model (i.e. higher levels of disturbance promote ruderal species with high rates of growth and seed production) and invasion ecology (exotic species commonly dominate the ruderal "increaser" category and dominate soil seed banks in degraded areas; Rejmanek 2000; Booth et al. 2003). In this case, however, seed densities of native and exotic species responded positively to site degradation, and the ruderal native *C. difformis* unexpectedly dominated the soil seed bank. Thus, the general pattern of higher seed densities of ruderal species in degraded areas is fully consistent with Grime's C-S-R model, despite our hypotheses of contrasting behaviours of native and exotic species not being fully met.

Seed densities in our study averaged 26 333 seeds m^{-2} over all sites, but densities varied 10-fold between degradation states, ranging from a mean of 5212 seeds m^{-2} in intact sites to 54 614 seeds m^{-2} in degraded sites. Seed densities in intact sites appear to be among the lowest, while densities in degraded sites were towards the highest recorded from temperate, semi-arid and arid grasslands, shrublands and woodlands in Australia (range ca. 5000-83 540 seeds m^{-2} ; Hodgkinson et al. 1980; McIvor 1987; Lunt 1990, 1997; Jones et al. 1991; Navie et al. 1996; Morgan 1998; Batson 1999; Meissner & Facelli 1999; Lodge 2001). A proportion of wetland seeds fail to germinate in any individual wetting event (Leck & Brock 2000) so all germination studies document only a proportion of the viable seed bank. In general, therefore, the results from our study indicate minimum estimates of seed abundances in the soil seed bank, and additional undocumented seeds are likely to have occurred in all degradation classes and microsites. Nevertheless, the methods used were successful in identifying differences in soil seed banks among degradation classes and microsites.

Conclusions

Overall, we detected little difference in abundance of seeds of native dryland species between degraded and intact sites. Further, degradation did not promote seeds of exotic dryland species to the same extent predicted in the literature, demonstrating the relatively high resilience of dryland soil seed banks in intermittently inundated wetlands. By documenting the potential resilience of intact and degraded floodplain woodlands, and potential regeneration of exotic and native plants in this fragmented ecosystem, the results from this study provide valuable information to guide management interventions and restoration efforts by land managers and ecologists.

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