

RESEARCH ARTICLE

Seed rain as a propagule source for restoration of semi-arid floodplain old fields

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Abstract

Aims: Revegetation of the world's abandoned agricultural land (old fields) is vital to promote biodiversity and restore ecosystem services. Natural regeneration, whereby vegetation regrows on its own via the propagules already within the landscape, is a cost-effective restoration approach for old fields. It is vital that we understand how different seed sources contribute to the regenerative capacity of old fields to make informed management decisions. Little is known about seed rain as a propagule source for restoration within semi-arid floodplains of eastern Australia.

Location: Within this study, we examined seed rain and extant vegetation in old fields and paired remnant sites across four regions in the northern Murray–Darling Basin, eastern Australia.

Methods: Seed rain was surveyed using seed traps that were then subjected to a seedling emergence experiment.

Results: Minimal differences in seed rain composition, species richness, abundance, and plant functional groups were observed between old-field and remnant sites, indicating similarities in seed dispersal within both land use histories. Larger distances to remnant patches and mean annual rainfall were found to drive the composition of old field's seed rain. The study found few emerged *Eucalyptus* seedlings despite seed traps being placed during peak seed release periods, which may be due to poor tree conditions from drought, interference with seed traps and the episodic germination requirements of *Eucalyptus coolabah*.

Conclusions: This study demonstrates that seed rain can contribute to the natural regeneration of understorey vegetation, with low abundances of exotic species, unlike other seed bank types. However, seed rain composition resembled little of the extant vegetation, suggesting a species pool facing barriers to germination and establishment, but likely linked to bet-hedging strategies. Moving forward to promote natural regeneration via seed rain in old fields, protecting existing patches of vegetation within the landscape is vital to enable biotic connectivity.

KEYWORDS

agricultural landscapes, natural regeneration, passive restoration, propagule bank, revegetation, seed rain, spontaneous succession

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1 | INTRODUCTION

Agricultural land abandonment (old fields) is increasing worldwide due to socioeconomic and environmental drivers (Cramer et al., 2008). These drivers include changes in environmental temperature and precipitation (Osawa et al., 2016; Horion et al., 2019), which are expected to be exasperated by climate change and further increase land abandonment (Benayas et al., 2007). The global distribution of old fields provides an opportunity for revegetation across vast areas and, therefore, the prospect of mitigating global declines in biodiversity (Isbell et al., 2019; Yirdaw et al., 2019) and carbon sequestration (Cheng et al., 2015; Nave et al., 2019). To revegetate old fields, it is critical to understand ecological dynamics mediating the effectiveness of restoration methods (Bowen et al., 2007; Hermy & Verheyen, 2007).

A continuum of restoration interventions can be applied to ecological restoration practices, ranging from unassisted recovery (i.e., natural regeneration) to intensively assisted recovery (Chazdon et al., 2021). On the far end of the continuum, intensively assisted recovery requires the reconstruction of major abiotic factors, such as topsoil replacement, hydrological modification and sculpting topographical features before biotic elements can be restored (Krishnan & Osuri, 2023). Moderately assisted recovery requires intervention regarding some biotic and abiotic components such as tree planting or seed sowing, tree thinning or topsoil amendment. It should be noted that success rates can be low if abiotic factors are not amended simultaneously with or before biotic factors to enable successful vegetation establishment (Clark et al., 2007; Silvestrini et al., 2012). If disturbances within the landscape hinder recovery, lightly assisted recovery methods may need to be integrated. These methods involve alleviating pressures such as excluding grazing animals, enhancing seed dispersal, and managing fire to facilitate recovery (Holl & Aide, 2011). Finally, recovery can proceed unassisted (i.e., natural regeneration) whereby revegetation occurs via establishment from the seeds within the landscape without any intervention (Prach et al., 2019). This continuum acknowledges that different approaches can have passive and active restoration elements depending on the extent of environmental degradation (McDonald, 2021).

Due to low levels of intervention, natural regeneration approaches can feasibly be applied at lower costs to large expanses of abandoned agricultural land (Geddes et al., 2011; Chazdon et al., 2021). Natural regeneration can provide a variety of positive outcomes for biodiversity, ecosystem services (Strassburg et al., 2016), the preservation of localised genetic diversity (Thomas et al., 2014), and a low-cost means of carbon sequestration (Evans et al., 2015). Moving forward under climate change, natural regeneration is increasingly vital as these ecosystems are likely to be more resilient to changing climatic conditions (Zivec et al., 2023b). Consequently, for natural regeneration to be an effective applied restoration method, it is imperative to understand the regenerative capacity of old fields in site-specific contexts. Understanding the biotic potential of ecosystems is vital information needed to make informed management decisions (Chazdon & Guariguata, 2016).

To holistically understand the regenerative potential of old fields, it is paramount to understand the relative contribution of all propagule sources and storages (de Paula et al., 2023). Seed can be stored within the soil, animal scat, leaf litter and aerial seed banks (Middleton, 2003; Zivec et al., 2023a). If limited seeds are stored within a location, there must be sufficient seed dispersal from the surrounding landscape for natural regeneration to occur (Kimmel et al., 2010). Seed rain is a source of the transient seed bank from the surrounding landscape transported via animals, wind and gravity. Scattered trees retained within agricultural fields (i.e., paddock trees) and nearby remnant vegetation are often an essential source of seed rain (e.g., Cubina & Mitchell Aide, 2001; Pangou et al., 2009). Paddock trees also facilitate regeneration by providing shade, soil moisture and bird perching sites, encouraging seed deposition through zoochory (Manning et al., 2006). Both paddock trees and patches of established vegetation have been shown to increase the rate of natural regeneration within landscapes (e.g., Neilan et al., 2006; Zivec et al., 2021).

Semi-arid floodplain ecosystems are subjected to many disturbances, such as extended dry periods punctuated by significant flooding events (Horner et al., 2012). Many plant species in semi-arid floodplain ecosystems have evolved life-history strategies to cope with the variability in such conditions, including the formation of persistent seed banks and employ ecological bet-hedging strategies (Catford & Jansson, 2014; Capon & Reid, 2016). Semi-arid floodplain trees such as *Eucalyptus camaldulensis*, *Eucalyptus coolabah* and *Eucalyptus largiflorens* are serotinous species (Jensen et al., 2008; Capon et al., 2016, p. 127). Serotinous species can retain some mature seeds within their canopy and release them as seed rain when conditions become favourable, such as when floodwaters recede (Jensen et al., 2008), to increase the chances of successful germination and establishment (Roberts & Marston, 2000).

This study focuses on the contributions of seed rain for natural regeneration in semi-arid regions of eastern Australia within different land-use histories, given that this represents a significant knowledge gap in the same context (Zivec et al., 2021, 2023a). Seed rain refers to propagules transported from the mother plant via wind, gravity or animals and is a source for vegetation assemblages in a variety of contexts (e.g., Pakeman & Small, 2005; Standish et al., 2007; Auffret & Cousins, 2011). Little is known about seed rain as a propagule source within semi-arid areas of eastern Australia and how extant vegetation contributes to this seed source. We sought to determine the environmental drivers of seed rain composition and structure and assess the relationship between seed rain and extant vegetation.

We considered the following research questions:

1. What is the species composition of seed rain within floodplain habitats, and how do they differ between land-use histories?
2. What is the relationship between seed rain and extant vegetation and their environmental correlates?
3. What are the key environmental factors driving variation in floodplain old-field seed rain?

2 | METHODS

This study was conducted in semi-arid regions across the northern Murray–Darling Basin (MDB) in eastern Australia (Figure 1). The northern MDB is hot and persistently dry (Walker et al., 1995), with rivers that have hydrological flows that are highly variable (Bunn et al., 2006). Study sites were selected around four northern MDB towns that represent an east-to-west aridity gradient: Bourke, St George, Mungindi and Moree (Figure 1, Table 1). At the time of this study, the northern MDB was experiencing a severe drought. The rainfall in the MDB was substantially below average from 2017 to 2019. These three years were the driest ever on record for any 36-month period, with some areas receiving the lowest-ever rainfall recorded per year in history (<100 mm) (Bureau of Meteorology, 2019, 2023).

Floodplain vegetation communities within this study are part of the endangered coolabah–black box woodland ecological community (NSW Government, 2023), typically characterised by a canopy of *Eucalyptus coolabah* Blakely & Jacobs (coolibah), *Eucalyptus camaldulensis* Dehnh (river red gum), and in some areas *Eucalyptus largiflorens* (black box), along with associated mid-canopy *Acacia* species. Where present, the shrub layer is dominated by *Duma florenta* Mesin (tangled lignum) (King et al., 2022). Understorey communities are typically highly variable and dynamic, responding to environmental conditions (Capon, 2005). During dry periods, the understorey is dominated by chenopod subshrubs (e.g., *Sclerolaena muricata* (Moq.)

Domin var. muricata), hardy and exotic forbs (e.g., *Medicago polymorpha* L. and *Portulaca* sp.) and perennial grasses (e.g., *Sporobolus* sp.) (Good et al., 2012). In wet times, the understorey exhibits a diversity of aquatic and terrestrial forbs, grasses, sedges and ferns such as *Marsilea drummondii* and *Cyperus difformis* L.

Indigenous Australians have long inhabited and managed the regions before Europeans arrived in the 1850s. At first, European settlers grazed large flocks of sheep, of which they would then transport wool along the Darling River (Gell et al., 2019). Extensive cropping did not escalate until the 1950s (Walker & Thoms, 1993). In the MDB, semi-arid floodplain ecosystems often coincide with vast agricultural areas of economic and ecological significance. In recent years, land use across the northern region has been a mix of irrigated and dryland cropping and livestock grazing. Extended drought impacts from climate change, land-use changes (i.e., conversion of cropping fields to conservation land or grazing) and greater environmental flow delivery causing increased inundation of floodplain crops have led to abandoned cropping fields within the study area (Docker & Robinson, 2014).

2.1 | Extant vegetation surveys

Sites were selected within floodplain areas in two land-use histories: remnant vegetation and old fields. Remnant vegetation was defined as an area that had never been used for cropping but may

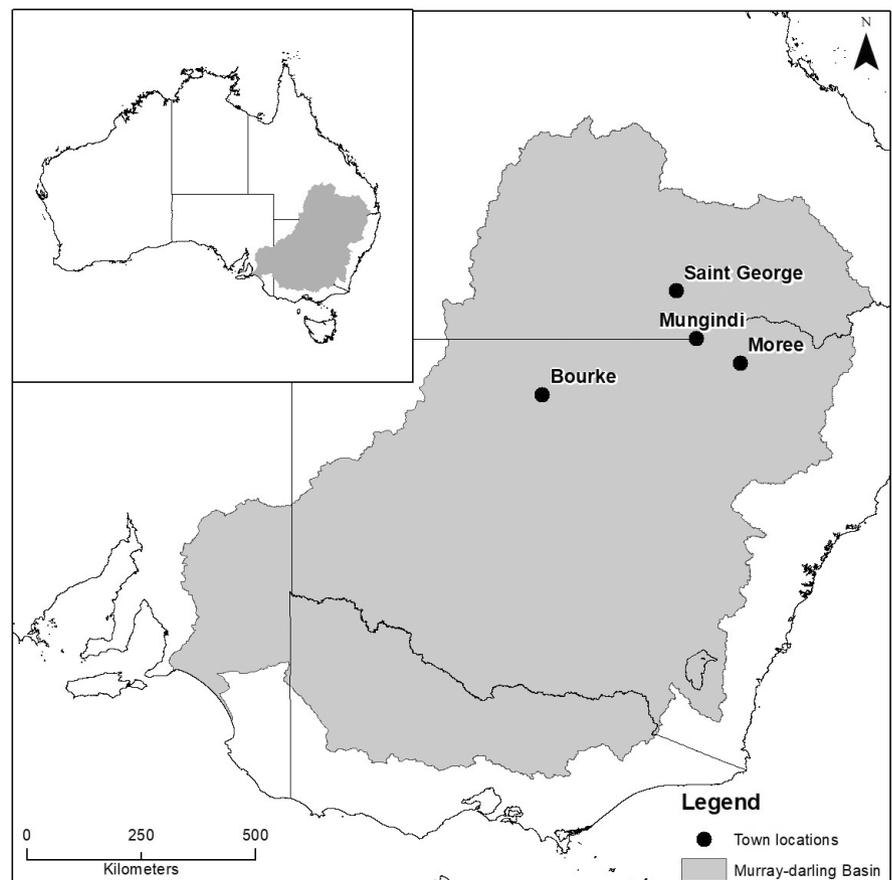


FIGURE 1 Map displaying the four major towns the study regions represent. Source: Zivec et al., 2021.

Regions	Age of old fields (m)	Previous agricultural land-use of old fields	Mean annual rainfall (mm) ^a	Max. and min. summer and winter temps (C°) ^a
Moree	33	Unknown cropping,	573.7	Summer: 34.3/20.5 Winter: 18.3/4.6
	7	Irrigated cotton,		
	20	Irrigated cotton		
Mungindi	5	Irrigated cotton,	504	Summer: 35.6/20.8 Winter: 19/4.7
	10	Irrigated cotton,		
	20	Unknown cropping		
St George	8	Unknown cropping,	460.8	Summer: 35.3/22.3 Winter: 19.7/5.3
	28	Unknown cropping,		
	33	Unknown cropping		
Bourke	9	Irrigated cotton,	307.1	Summer: 37.6/22.8 Winter: 18.6/4.2
	9	Irrigated cotton,		
	40	Dryland wheat		

Note: The average maximum and minimum summer and winter temperatures are the average maximum and minimum temperatures during the recorded period for summer in January and winter in July. Moree mean annual rainfall and temperatures are from 1995 to 2022. Mungindi's mean average rainfall and temperature are from 1991 to 2022, St George's mean rainfall and temperature are from 1997 to 2022, and Bourke's mean average rainfall and temperature are from 1998 to 2022.

^aSource: Bureau of Meteorology (2022a, 2022b, 2022c, 2022d).

have been grazed by livestock. Old fields were defined as areas that had been previously cropped but subsequently abandoned from cropping for more than five years and may also have been grazed by livestock. All sites were selected within cotton-growing farms, where livestock is only intermittently grazed for land management, with heavy stocking not occurring in recent history. Feral and native grazing animals are also managed within cotton farms for crop and land protection. A paired-site design was used; therefore, for every old-field site, a remnant site was selected within close proximity to be used as a reference condition. Paired sites were always selected on similar soil types, such as black cracking clay, with similar dominant overstorey species (*E. coolabah* and *ca-maldulensis*), and large-scale flooding history is similar due to their close proximity. We defined an old field and its remnant pair as a 'location'. Within each location, we surveyed three 50 m × 50 m plots within each land-use history. In total, there were 12 different locations and three within each region. Therefore, there were 72 plots, with 36 in each land-use history.

Within each plot, understorey vegetation and environmental characteristics were surveyed within ten randomly placed 1 m × 1 m quadrats. All understorey vegetation, including ground cover, seedlings, and shrub species, was identified within this quadrat, and species' per cent cover was estimated. A shrub was defined as a woody plant with multiple small stems with diameter at breast height (DBH) under 5 cm and up to 2 m tall. A seedling was defined as a tree which was under 1 m tall. The canopy cover was recorded using a spherical densitometer in all four directions of the compass at each quadrat. An overstorey vegetation survey was also conducted within each plot, with all trees counted and identified and their height and DBH recorded. Distance to remnant patch was calculated from the middle of each old-field plot,

where a GPS location point was measured infield, to the nearest patch of remnant vegetation (two or more large established trees) as determined from a remotely sensed image from Google Earth Pro. These two or more trees can be a cluster of paddock trees, or a more extensive patch of remnant vegetation. Distance to remnant patch varied from 25 to 463 m (Appendix S1). Paddock trees per plot were calculated by summing the total number of trees over 30 cm DBH. For more information regarding the standing vegetation, site characteristics and selection process, please see Zivec et al., 2021.

2.2 | Sample collection

A propagule trap was placed on the ground at the centre of all 72 plots (36 remnant and 36 old fields). A propagule trap was a piece of artificial grass mat of 0.5 m × 0.5 m (Gough et al., 2015). The trap was pegged to the ground on all four sides to prevent it from being moved by wind and dislodging any seeds captured. Rain events and insect interference on the seed traps throughout the study were considered part of natural dispersal modes. However, we acknowledge how these processes may have impacted the results within the discussion. In total, 31 remnant and 22 old-field propagule traps were successfully retrieved from ten old-field and 11 remnant sites. Please see Appendix S1 for more details regarding the location of the retrieved traps. The propagule traps were collected completely dry, placed into individual plastic bags and transported back to facilities at Griffith University. Seed traps were stored in sealed plastic bags in dark containers in a temperature-controlled lab at 22°C until the seedling emergence experiment commenced.

TABLE 1 Key information regarding the study sites within each region.

Understorey vegetation seed production in the region is episodic, typically occurring after hydrological events such as rainfall and flooding. Although rainfall and flooding events are highly variable throughout the northern MDB, with multiyear dry spells and droughts a regular occurrence, hydrological input is primarily driven by subtropical rainfall between January and March (Capon, 2005; Bureau of Meteorology, 2019). Overstorey species *E. coolabah*, *E. camaldulensis* and *E. largiflorens* are serotinous, meaning they can retain some mature seeds within their canopy, and release can be triggered by environmental cues such as hydrological events, although *E. camaldulensis* is known to have peak seed release from December to March, *E. largiflorens* from October to March and *E. coolabah* from April to August (Jensen et al., 2008; Kerr et al., 2024). Propagule mats were left for 6 months between January 2019 and July 2019, as this coincides with the most probable time to capture understorey and overstorey species seed rain within both summer and winter.

2.3 | Seedling emergence trials

Plastic containers measuring 172 mm in length, 120 mm in width, and 100 mm in depth, each with four drainage holes, were used for the seedling emergence trials. Containers were filled with 2 cm of vermiculite and 4 cm of seed-raising mix. The seed-raising mix comprised fine composted bark, sphagnum peat and coir. Each plastic bag that contained the seed traps was emptied, and each seed trap was swept with a paintbrush and then visually inspected to ensure all material was removed. Each seed rain sample was placed in its own container on top of the seed-raising mix. Any significant bits of bark, sticks or stones were removed from the container prior to the commencement of the experiment.

Each container was placed into the Griffith University glasshouse facility. Samples were watered regularly and were kept damp for the entire experiment. Ensuring damp soil has previously been shown to encourage the most diverse expression of semi-arid floodplain seed banks (Casanova & Brock, 2000; Capon, 2007). Previously, no differences have been found in seed density or species richness of seed banks between seedling emergence and seed identification in semi-arid ephemeral wetlands; therefore, the seedling emergence technique was chosen. However, it is important to note different species may be detected using alternative methods and this can influence the species composition identified within the data (Price et al., 2010). The position of containers was rotated within the glasshouse every week to account for any potential inequalities in sunlight, and the growth period lasted 12 weeks, from 8 December 2019 to 8 March 2020. As seeds germinated, they were removed, identified and recorded. All species names follow the nomenclature provided by NSW Flora Online (<https://plantnet.rbgsyd.nsw.gov.au>). During the experiment, the average maximum temperature was 47°C and the minimum 20°C, similar to the on-ground temperatures observed within the surveyed regions (Cleverly et al., 2016).

2.4 | Data analysis

All species were assigned to the following plant groups; forbs, grasses, exotic species, woody species and sedges and rushes (See Appendix S2). Abundance was calculated by totalling the number of emerged seedlings per experimental container or from each plant group per container. Species richness was calculated as the total number of different seedling species within each container. A linear mixed-effects model was used to explore differences in the extant vegetation characteristics, with the data transformed where necessary to meet the model's assumptions. A generalised mixed-effects model explored differences between species richness and abundances from different land-use histories. Land-use history (old field and remnant) were fixed factors, while region and location were used as random effects, with location nested within the region. Quasi-Poisson distribution was used to detect significant differences (Potts & Elith, 2006). Species traits, particularly the characteristics of propagule dispersal modes, were investigated using the AusTraits database (Falster et al., 2021).

The composition of the emerged seedlings within each land-use type and between regions was explored using non-metric multidimensional scaling (nMDS) ordination using a Bray–Curtis distance matrix. Prior to MDS analysis, the replicate plots for each location were averaged, so there was one old field and one remnant value for each species at each location. To meet the assumption of homogeneity, nMDS data was square-root-transformed or converted to presence/absence. An analysis of similarity was used to test differences between the community composition of emerged seedlings between land-use histories and regions. In order to relate the compositional differences of old-field emerged seedlings to habitat conditions, a distance-based redundancy analysis (RDA) was performed. The species abundance data were Hellinger-transformed and the explanatory factors were standardised to zero and unit variation due to their differences in physical units. A stepwise forward selection model-building approach was completed if an RDA model tested was significant. Only significant terms were kept in the model (significance level $p < 0.05$). An ANOVA on 999 permutations was used to test the final model with all significant terms (Legendre & Gallagher, 2001; Borcard et al., 2011). The multivariate analyses were undertaken in the *vegan* package (Oksanen et al., 2019) within the R program (Version 4.1.2, R Development Core Team, 2021).

3 | RESULTS

3.1 | Seed rain characteristics

In total, 760 seedlings emerged from 38 different species from the seed rain (Appendix S3). The most common species that emerged from the seed rain was *Portulaca oleracea* (203), a common forb species, followed by *Ammannia multiflora* (185). Of the emerged seedlings, 24 taxa (63%) were from the forb plant group, followed by four

sedges and rushes (10%), five woody taxa (13%) and four grasses (10%). Of the woody taxa, ten trees emerged: nine *Eucalyptus* seedlings and one *Acacia* seedling. The rest were from the shrub or subshrub group. Twenty-seven seedlings (3%) from ten different taxa could not be identified to the species level, only to plant functional groups. In total, 57 out of 733 (7%) seedlings from seven out of 28 (25%) species identified to the species level were exotic. Most exotic

seedlings emerged from the forb group, with no woody exotic species emerging from the seed rain.

A total of seven exotic species were identified to the species level in the seed rain. Of these, six species were present in both the old-field and the remnant vegetation, and an additional exotic species was recorded exclusively in the old field. Eighteen species emerged from both land-use histories, while 12 species only

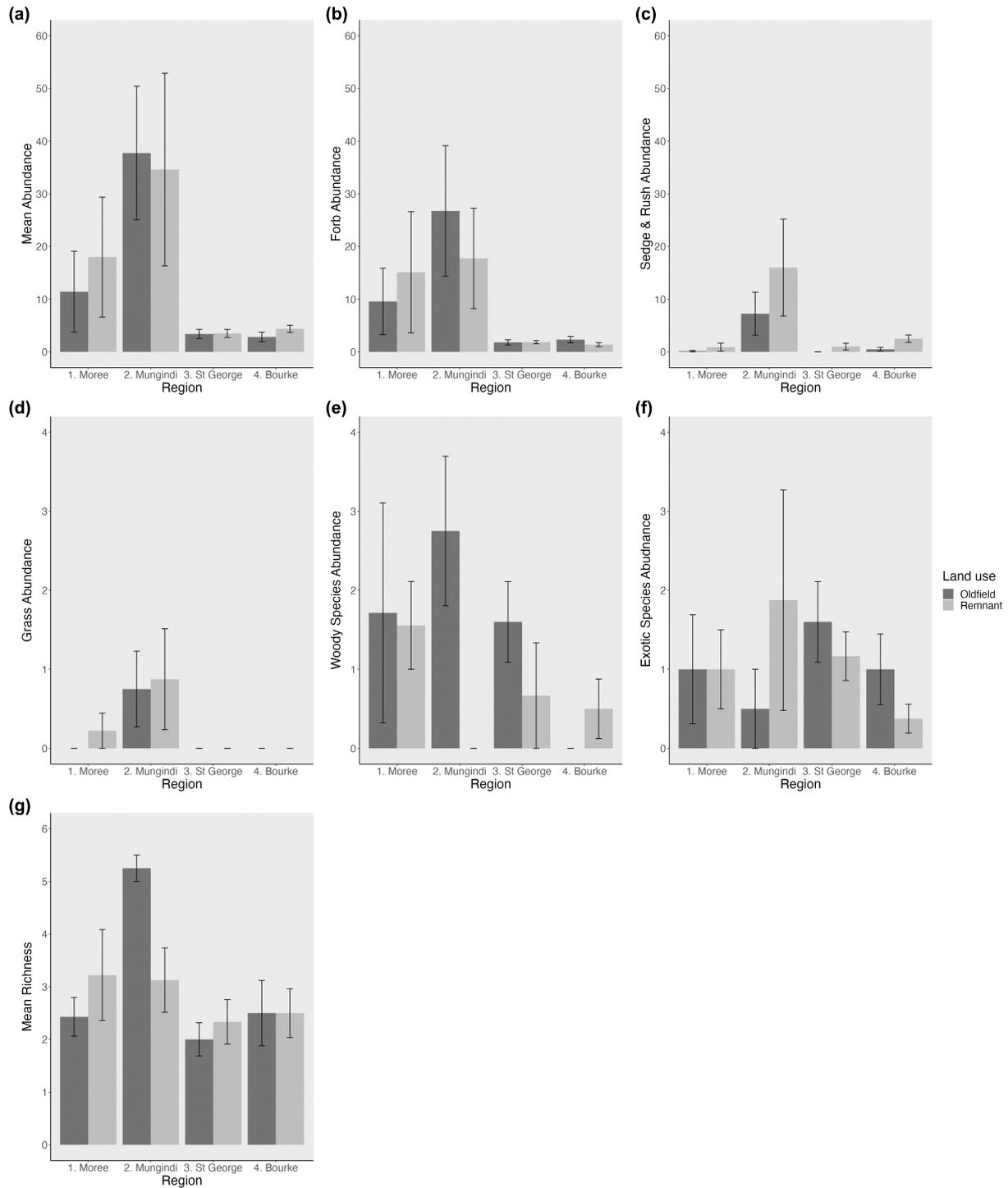


FIGURE 2 Mean values of emerged seed rain across different land-use histories and regions, showing (a) abundance, (b) forb abundance, (c) sedge and rush abundance (significant), (d) grass abundance, (e) woody species abundance, (f) exotic species abundance, (g) mean richness. Error bars display standard error.

emerged from remnant seed rain and eight only from old fields. All the trees that emerged came from the same paired remnant and old-field site in St George. Overall, there were very few significant statistical differences between old fields and remnant sites seed rain (Figure 2, Table 2). No significant difference existed between the seed rain's total abundance, species richness and abundance of exotic species between land-use histories. No difference was observed in plant groups between land-use histories for forbs, grasses, and woody species. However, there was a significant difference between sedges and rushes, with more emerged seedlings from remnant areas ($p=0.001$).

3.2 | Extant vegetation characteristics and relationship to seed rain

A total of 103 species were present within the overstorey and understorey extant vegetation. Of these, 78 species were in the understorey, 25 in the overstorey, and five species were found in both categories, represented as tree seedlings within the understorey. Of the 25 overstorey species, only one was exotic. The most common overstorey species was *Eucalyptus coolabah*. The most common

understorey species was *Sclerolaena muricata*, followed by *Einadia nutans*, both of which are small subshrubs from the Chenopodiaceae family. Within the understorey, there were 41 forb species (53%), 22 woody species (28%), 13 grasses (17%) and two sedges (2%). Within the understorey, 17 out of 78 (21%) species were exotic; 11 were forbs, four were woody, one was a sedge, and one was a grass.

Land-use history had a noticeable impact on canopy cover ($p \leq 0.001$ and marginal $R^2=0.366$), with remnant plots exhibiting significantly higher canopy cover than old fields. While there was no difference between the percentage of ground cover between old fields and remnant sites, there is a clear east-to-west aridity gradient between study regions (Figure 3).

The composition of emerged seedlings from the seed rain between remnant and old-field areas was not found to be significantly distinct (p -value=0.073, $R=0.1147$), despite most of the remnant sites being positioned high on Axis 2 and old fields lower on Axis 2 (Figure 4a). The assemblages of the seed rain, understorey and overstorey were all completely distinct (p -value=0.001, $R=0.6951$), with no overlap between vegetation types (Figure 4b).

Thirteen out of 128 taxa were shared between the extant vegetation (understorey and overstorey) and the emerged seed rain. This included eight native and five non-native species. Most of these species

TABLE 2 Regression and significant values of the models' terms testing the influence of land-use histories on the response variables.

Response variable	Fixed effect	Estimate	SE	p-value
Total abundance	Old field:Remnant	0.3685798	0.2613937	0.1661
Species richness	Old field:Remnant	-0.0199718	0.1552572	0.8983
Forb abundance	Old field:Remnant	0.1074537	0.3060895	0.7273
Grass abundance	Old field:Remnant	-0.745041	0.6200134	0.2364
Sedges and rushes abundance	Old field:Remnant	1.503564	0.3097865	>0.000
Woody species	Old field:Remnant	-0.6336020	0.4255502	0.1442
Exotic species	Old field:Remnant	0.04792156	0.4836112	0.9215

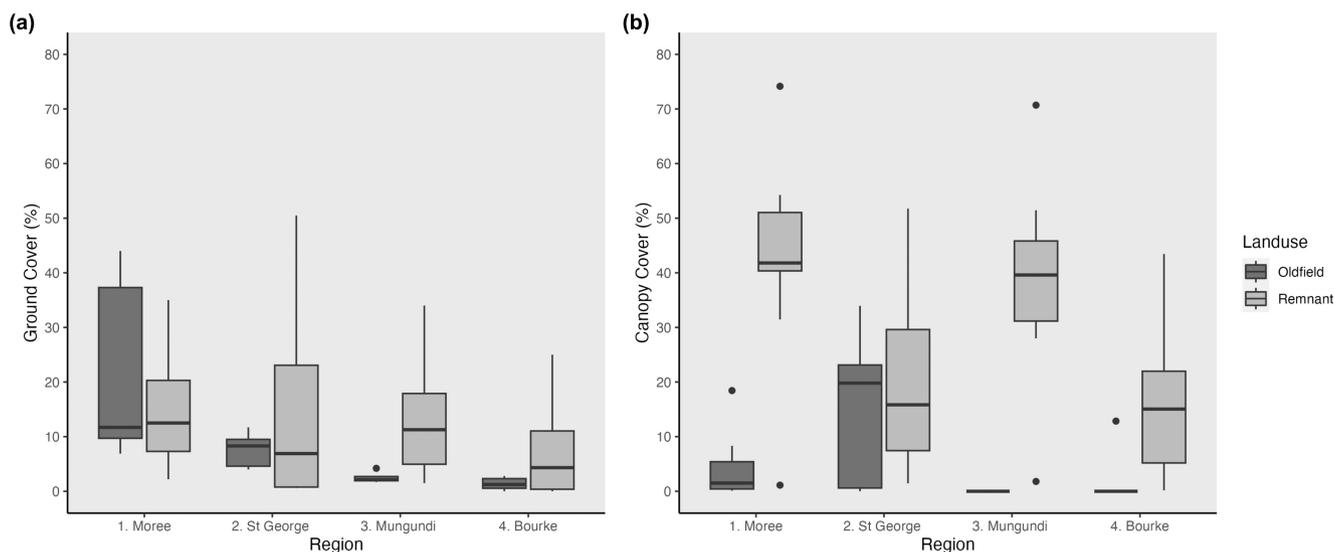


FIGURE 3 Boxplot displaying old-field and remnant vegetation within different regions of the study area's (a) ground cover (%) (b) canopy cover (%).

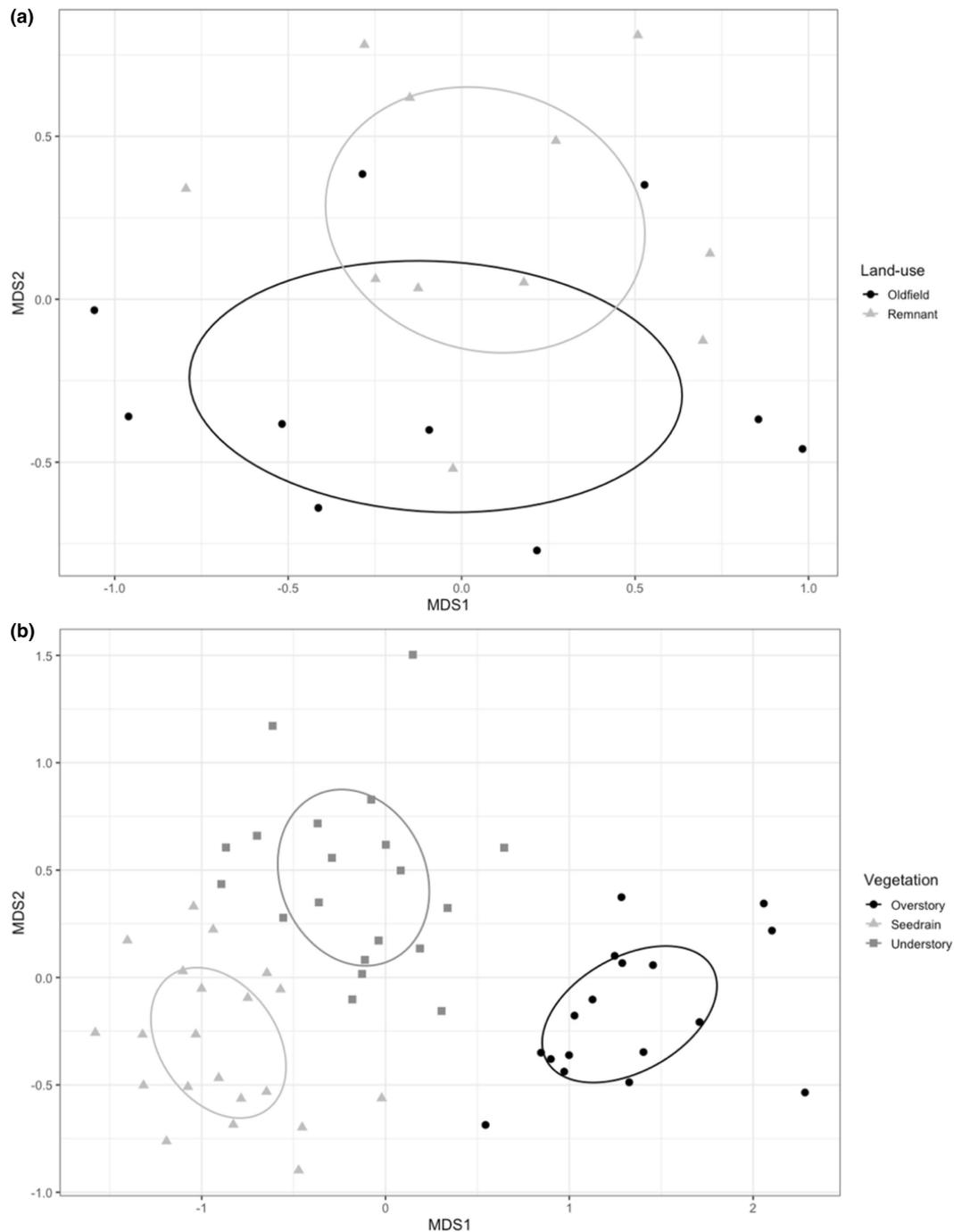


FIGURE 4 Non-metric multidimensional scaling ordination. (a) Emerged seed rain assemblage by land-use (stress=0.17); (b) assemblage of emerged seed rain, extant understorey and overstorey vegetation (stress=0.10).

were forbs (ten species), with one woody species, one sedge and one grass. Of the taxa identified to the species level, 16 out of 28 (57%) were only found within the seed rain (Appendix S4). Six of these species were non-native (five forbs and one grass). Of the species recorded only within seed rain and identified to the species level, seven were dispersed primarily by aerial modes such as barochory or anemochory, with seed movement likely at the site or local scale. While six were dispersed primarily by zoochory and epizoochory, one species (*Cyperus difformis*) is typically dispersed by water, and has the capacity for more extensive

landscape distance dispersal. Finally, two species (*Tribulus terrestris* and *Eragrostis setifolia*) are dispersed aerially and via animal modes, capable of local and landscape-scale dispersal.

3.3 | Drivers of seed rain composition

The RDA analysis indicated that significantly correlated environmental and landscape variables explained 16% of the total variation

in the composition of the old field's seed rain (Table 3, Figure 5). The variation in the composition of old fields' emerging seedlings was significantly associated with mean annual rainfall and distance to remnant patch. It is apparent in Figure 5 that the distribution of samples along Axis 1 reflects a clear aridity gradient. Moree samples (the wettest) clustered low on Axis 1, with Bourke higher (the driest) and St George scattered between the two. Two Mungindi sites have the highest distances from remnant patches (Appendix S1), with this shown to be a significant driver of the species composition along Axis 2 (Figure 5).

4 | DISCUSSION

Semi-arid floodplains exhibit highly diverse, large and long-lived seed banks (James et al., 2007). This enables species to persist during dry periods and surge in diversity when favourable conditions arise, exhibiting the boom-and-bust nature of arid ecosystems (Bunn

TABLE 3 RDA model results regarding analysing emerged seedlings from the seed rain with environmental variables. NS represents the factors that were not significant.

Explanatory variables	Variance	F	p
Time since abandonment	NS	NS	NS
Mean annual rainfall	0.065	1.73	0.037
Distance from remnant patch	0.07440	1.96	0.008
Canopy cover	NS	NS	NS
Number of paddock trees	NS	NS	NS
% Ground cover	NS	NS	NS

et al., 2006). While some studies have investigated aerial seed banks of key *Eucalyptus* species in semi-arid floodplains (Dexter, 1978; George, 2004; Jensen et al., 2008), few studies have looked at the overall species composition of the seed rain and its contribution to natural regeneration of old fields (Standish et al., 2007). This study found that seed rain in semi-arid floodplains of eastern Australia displays minimal differences between land-use histories and contains few exotic species, demonstrating seed rains' importance for seed dispersal throughout the landscape.

In eastern Australian semi-arid landscapes, disturbance from previous cultivation can be significant due to slow recovery times caused by low rainfall and poor soil nutrients. However, the few observed differences in the seed rain between old fields and remnant sites indicate that ecosystem processes drive biotic resilience despite the challenging environmental conditions (Cramer et al., 2008). Despite the drought conditions, the seed rain observed within this study demonstrates a continuous supply of seeds dispersing via animals and wind, which was similar in both land-use histories. There are flocks of nomadic and local birds, kangaroos and ants that are abundant within the landscape, all able to contribute to this seed dispersal (Gove et al., 2007; Jordan et al., 2017; Zivec et al., 2023a). Distance to remnant vegetation patch was an essential factor underpinning the species composition of seed rain in old fields, with areas furthest away from remnant patches exhibiting unique assemblages (Martínez-Garza et al., 2009). The important input from existing vegetation into old fields drives the homogenisation of community composition between the two land-use histories. These results highlight the importance of keeping patches of existing vegetation within the landscapes to improve the biotic resilience to land-use change (Pardini et al., 2010).

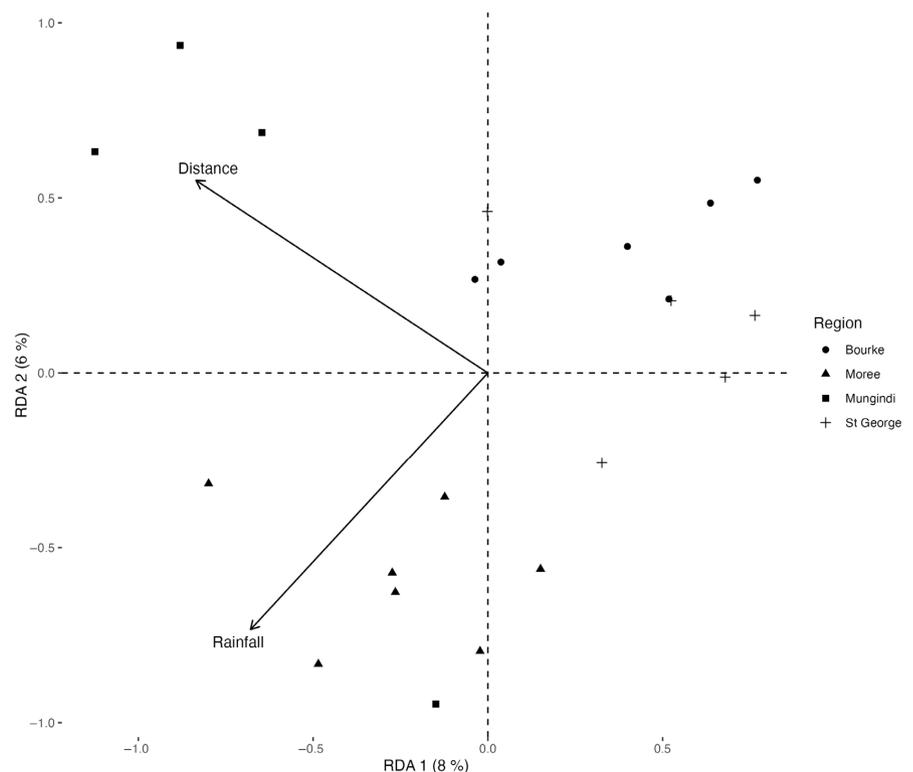


FIGURE 5 Triplot representing how emerged seedlings from old fields' emerged seed rain are influenced by different environmental variables. Scaling 2 was used; therefore, the distance between objects is not approximate, and the angle between vectors reflects linear correlation.

This study found low numbers of *Eucalyptus* tree seedlings, and of the few that did emerge, all came from a single paired old-field and remnant site. This was even despite seed traps being placed in sites during peak times of seed release for the dominant overstorey *Eucalyptus* species. The low number of emerged seedlings may be attributed to poor tree conditions due to the drought experienced during the experimental period (Jensen et al., 2008). However, the low numbers of emerged trees observed may also be attributed to insect predation from the seed traps or interference from rainfall events. Finally, the successful germination of the dominant overstorey species, *E. coolabah*, can be highly episodic, requiring a unique set of conditions (Vincent et al., 2018). Conditions within the glasshouse may not have been optimal; therefore, seeds may have been within the seed rain but not present in the seedling emergence experiment. Therefore, these results should be interpreted cautiously and highlight the importance of more knowledge about the conditions required to germinate dominant *Eucalyptus* species within the MDB (Good et al., 2013).

Floodplains are susceptible to species invasions due to interactions between the traits of exotic species and landscape features, particularly with hydrological input (Catford & Jansson, 2014). Soil seed banks in semi-arid floodplain regions of Australia have been found to contain high abundances of exotic species (e.g., Greet et al., 2013; Dawson et al., 2017). Soil, scat and litter seed banks investigated in the same sites found a high proportion of emerged seedlings were exotic (28%) (Zivec et al., 2023a). However, our findings from the seed rain indicate a relatively low representation of exotic species (7%). This research is the first to investigate seed rain within these landscapes and demonstrate its low abundance of exotic species, indicating that it is not a large contributor to species invasion within floodplain ecosystems during dry periods. This further highlights the importance of seed rain for distributing native seeds throughout the landscape and consistently contributing to old field's biotic capacity to recover (Martínez-Garza et al., 2009).

There was little overlap between extant vegetation and the species found in the emerged seed rain, suggesting that seeds may be facing barriers to successful germination and establishment (Buisson et al., 2006; Dosch et al., 2007). This lack of overlap is likely due to the extreme drought conditions present at the time of sampling, with species in the seed rain potentially employing bet-hedging strategies to enhance ecological fitness (Clauss & Venable, 2000). Ecological bet-hedging is a survival mechanism employed by arid plants to cope with unpredictable and stressful environments, such as those in the northern MDB (Peters et al., 2011). The seeds dispersed in the seed rain act as a reserve of dormant seeds, which will germinate when favourable conditions, such as rainfall or flooding, occur. The seed rain had a high proportion of species with wind or animal dispersal modes, demonstrating both landscape and local transport of seeds. These seed dispersal processes increase the genetic diversity of vegetation biodiversity and ensure species colonisation in new areas, while not being a significant distributor of exotic species in this circumstance (Ozawa et al., 2013). Landscape

biotic resilience is increasingly important under climate change due to shifts in agricultural demands and areas that are no longer feasible for agricultural production being converted back to land for nature (Zivec et al., 2023b).

The seed rain in this study exhibited clear patterns of regional heterogeneity and an aridity gradient. Patterns of species seed rain composition were driven by mean annual rainfall, with assemblages showing a gradient from areas of highest average rainfall to the lowest and an east-to-west gradient. Annual rainfall plays a crucial role in determining species' emergence from seeds and the resulting community assemblage, particularly in arid environments, as it strongly influences plant establishment, reproduction, and the traits that allow species to persist (Shriver, 2017). Areas of higher rainfall influence the species that can produce seeds and be dispersed via seed rain (Cleland et al., 2013).

Our study found that seed rain has the potential to contribute to the regeneration of understorey vegetation through both local and landscape-scale seed dispersal, with a minimal presence of exotic species. Even under the drought conditions during which this experiment was conducted, seeds were still produced and dispersed via seed rain, ensuring a continuous supply of seeds for understorey vegetation. The little representation of extant vegetation species in the seed rain demonstrates some barriers for successful germination and establishment, likely due to semi-arid plants employing bet-hedging strategies during drought to ensure ecological fitness during favourable hydrological input (Clauss & Venable, 2000). The contribution of seed rain to regeneration of woody species may be temporally and spatially dynamic, with seed dispersal and production closely linked to conditions such as drought, rainfall and flooding (Jensen, 2008). Land-use history did not impact the compositions or abundances of seed rain, demonstrating the effective seed dispersal via seed rain within both land-use histories. Distance to remnant patches of vegetation was shown to drive the composition of old-field emerged seed rain; therefore, land managers should prioritise protecting existing vegetation (Wijedasa et al., 2020).

AUTHOR CONTRIBUTIONS

Peta Zivec was involved in the conception, experimental design, fieldwork, data analysis, writing, and editing of the paper. Jaiden Johnston-Bates was involved in running seedling emergence trials, analysing data, and writing and editing the paper.

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CONFLICT OF INTEREST STATEMENT

The authors do not have any conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data sets related to this study are available at <https://doi.org/10.5281/zenodo.10556614>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Total number of seed traps collected at each site.

Appendix S2. Plant group categories.

Appendix S3. List of all species present within each seedbank, vegetation type, and land-use history.

Appendix S4. Identified species traits of emerged species only found in the seed rain.

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