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Perennial plant patches are sinks for seeds in semi-arid woodlands in varying condition

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32

33 **Key Words:** Patch type, seed bank, grazing, plant traits, richness, density, resilience
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37

38 **Abstract**

39

40 **Questions:** Understanding the processes that influence resilience in semi-arid woodland

41 communities is of critical importance in landscapes where livestock grazing is the dominant land

42 use and an important driver of site condition. Seed banks are a critical component of site resilience

43 as their persistence can be crucial for recovering from disturbances. We predicted that site

44 condition and landscape structural elements (perennial plant patches) would strongly influence the

45 richness and density of the soil seed bank.

46

47 **Location:** NSW, Australia

48

49 **Methods:** We conducted a seedling emergence study to investigate the germinable seed bank in

50 semi-arid woodland. Soil samples were collected from three woodland communities (Cypress

51 pine, Black box, Red gum) from sites in three levels of site condition (poor, average, good) and

52 from four patch types (tree, shrub, grass, open). Seed bank species were assigned to three plant

53 trait groups based on 1) origin; 2) lifespan and 3) palatability. We used linear models to assess the

54 effects of community, site condition and patch type on the richness and seed density of the

55 germinable seed bank.

56

57 **Results:** Site condition did not affect the seed bank density or richness, except for a lower density

58 of highly palatable species at poor condition sites. Across all communities the importance of patch

59 type on the soil seed bank density and richness varied with plant traits. The seed bank of perennial

60 plant patches had a greater density of perennial species, a lower density of low palatability plants,

61 and a greater richness of native and perennial species than interspaces.

62

63 **Conclusions:** Our results demonstrate that the germinable soil seed bank in semi-arid woodlands

64 can be relatively resilient to degradation. This suggests that disturbed sites where perennial

65 patches remain, may still have the ability to recover, because these patches act as important seed

66 reservoirs.

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70

71 **Introduction**

72

73 Both theoretical predictions and empirical studies demonstrate that a patchy distribution of
74 resources is critical for the functioning of arid and semi-arid systems (drylands; Noy-Meir, 1973).
75 Fertile, resource-rich patches dominated by trees, shrubs or perennial grasses, ameliorate
76 environmental conditions beneath their canopies (Howard, Eldridge & Soliveres, 2012), with high
77 infiltration rates (Vandandorj, Eldridge, Travers, Val & Oliver, 2016), and a large diversity of
78 microbes (Bachar, Soares & Gillor, 2012), creating ‘safe sites’ for seeds (Kinloch & Friedel,
79 2005). Perennial patches contrast markedly with sparsely vegetated open interspaces (inter-patch
80 matrix) as they capture resources such as water, sediment, seeds and nutrients that are that readily
81 shed from the interspaces (Ludwig, Wilcox, Breshears, Tongway & Imeson, 2005). The
82 movement of these resources sustains perennial patches in the landscape by reinforcing positive
83 feedback mechanisms, which support several key ecosystem processes. This finely balanced
84 resource regulation is susceptible to disturbance by anthropogenic activities such as land clearing
85 and overgrazing by livestock (Dreber & Esler, 2011) which in turn affects ecosystem functions.

86

87 Degradation processes, such as overgrazing (Tongway, Sparrow & Friedel, 2003) typically alter
88 both perennial patch size and their spatial distribution (Onatibia, Luciano & Aguiar, 2018).
89 Reductions in the size and cover of perennial patches are symptomatic of declines in ecosystem
90 health, and the capacity of sites to perform key functions such as nutrient cycling and infiltration
91 or sustain diverse plant communities. Changes to patch composition, size and configuration also
92 affect soil seed banks (Chambers & MacMahon, 1994) by altering seed capture, the supply of
93 water and sediments, and environmental conditions within the patch. In turn, this has the potential
94 to affect seed viability and seed longevity (Chambers & MacMahon, 1994), germination success
95 (Facelli & Brock, 2000) and seed production (Peart, 1989).

96

97 Although there are many ways in which prolonged livestock grazing can alter vegetation and
98 subsequently, the seed bank, the plants that are able to germinate from the seed bank are critical
99 for the post-disturbance recovery. There are several broad factors that determine how a site
100 responds to, or recovers from, disturbance including: 1) species composition and abiotic structure
101 of a site (hereafter ‘Community’), 2) site health or condition (hereafter ‘Condition’), which

102 depends on factors such as the morphology of the soil surface, the number of introduced species,
103 and the presence of a diverse range of perennial patch types and sizes, and 3) the traits of the
104 plants themselves (hereafter ‘Traits’), such as size, longevity, morphology or palatability (Diaz et
105 al., 2005; Leder, Peter, Funk & Peláez, 2017; Eldridge & Simpson, 2002), which affect their seed
106 shape, size, persistence within the landscape. For example, seed banks in communities with loamy
107 soils may be highly dependent on a continuous cover of biocrusts (Havrilla et al., 2019), which
108 dominate open areas, whereas those on clay soils might be more dependent on microsites
109 associated with patches of perennial plants. Small-seeded annual plants tend to dominate open
110 areas whereas large seeded perennial species thrive in stable perennial patches (Reichman, 1984;
111 Rolhauser, D’antoni, Gatica, & Pucheta, 2013; Peart, 1989). Also, long-term grazing by
112 introduced livestock can alter species composition and the persistence of highly palatable plants
113 within the landscape. Understanding how different site conditions and patch structure affect seed
114 bank structure is critically important because it provides insights into the likely changes that might
115 occur with increasing degradation such as prolonged livestock grazing (resistance), and the
116 likelihood that the site will recover from disturbance (resilience). Assessing the ability of a site to
117 recover from grazing, particularly among sites with varying land use histories and levels of
118 disturbance, is critical for the sustainable management of vegetation communities.

119
120 Here we report on a study where we investigated the effects of site condition and perennial patch
121 type on the density and composition of the soil seed bank of three widespread semi-arid woodland
122 communities. We had five hypotheses related to site condition, vegetation community and
123 perennial plant patches. (1) seed bank traits differ among the three communities due to differences
124 in soils (e.g. clay content) or topographical position in the landscape, (2) seed bank richness and
125 density vary with site condition because seed production and dispersal are affected by changes in
126 condition declines (Farrell, Hobbs & Colmer, 2012); (3) seed bank composition becomes more
127 homogeneous with declining condition; (4) seed bank density and richness are greater in vegetated
128 (tree, shrub, grass) patches than the interspaces because perennial patches act sinks for seeds and
129 sites of seed replenishment (Caballero, Olano, Escudero, & Loidi, 2008), and (5) the seed bank
130 from the interspaces is dominated by exotic, annual or unpalatable species, many of which have
131 small seeds that disperse easily and are captured in cracks and depressions in interspace soils
132 (Dreber & Esler, 2011).

133

134 **Methods**

135 *Study sites and site condition classes*

136 Three vegetation communities were selected for our study based on the overstorey dominance of
137 three focal tree species; Black box (*Eucalyptus largiflorens*), Cypress pine (*Callitris glaucophylla*)
138 and Red gum (*Eucalyptus camaldulensis*). Study sites were located in central and southern NSW
139 where the climate is typically Mediterranean, with slightly more rainfall during the six warmer
140 months in the east-central and during the cooler months in the south and south-west. Annual
141 rainfall ranged from 385 to 460 mm yr⁻¹ and average temperatures were about 18°C. Soil textures
142 ranged from sandy clay-loams in Cypress pine to silty loams in Black box and Red gum
143 communities. The Cypress pine community occurs on colluvial plains, sandy rises and source-
144 bordering dunes. The Black box community occurs on the upper level floodplains of inland rivers,
145 lakes and swamps and receives infrequent flooding, while Red gum community occurs adjacent to
146 major river systems and are subject to more frequent flooding.

147

148 Fifty-four sites were selected from a pool of 451 sites from a larger study that investigated the
149 effects of grazing on soil health and above-ground plant composition and structure in the same
150 three vegetation communities (Eldridge, Delgado-Baquerizo, Travers, Val & Oliver, 2017,
151 Eldridge et al., 2018; Travers, Eldridge, Dorrough, Val & Oliver, 2018; Travers, Eldridge, Val, &
152 Oliver, 2019). These studies revealed direct and indirect effects of grazing on soil health (Eldridge
153 et al., 2017), native and exotic plant richness (Eldridge et al., 2018), plant composition (Travers et
154 al., 2018) and mid-story vegetation structure (Travers et al., 2019). We used the findings of these
155 studies to select six poor, six average and six good condition sites in each of our three vegetation
156 communities. Condition classes were based on soil surface condition, native and exotic plant cover
157 and livestock grazing intensity (assessed *via* livestock dung and track density, see Eldridge et al.,
158 2017). Good condition sites had four key features: (i) high values of soil surface condition with
159 extensive cover of litter and biocrusts, and low levels of erosion; (ii) plant composition dominated
160 by native species with a mix of annuals and perennials; (iii) abundant large perennial grasses; and
161 (iv) relatively low levels of recent (dung counts) or historic (stock tracks) livestock grazing.

162

163 *Soil seed bank collection and seedling emergence*

At each site we established a 200 m transect with five points marked at 0, 50, 100, 150 and 200 m. At each point we selected the nearest of each of three patch types (tree, shrub and perennial grass) and then selected an inter-patch (open) adjacent to these, dominated by bare soil. Across the three communities, shrub patches were dominated mainly by the shrubs *Acacia* spp., *Dodonaea viscosa*, *Eremophila sturtii* and *Senna artemisioides* subsp. *artemisioides* and grass patches by the grasses *Austrostipa scabra*, *Aristida behriana*, *Rytidosperma caespitosum* and *Enteropogon acicularis*. We collected two soil core samples to 5 cm deep within/adjacent to each patch at each point along the transect. A total of 40 cores was collected per site, 10 cores from each patch type. The cores from each distance were pooled to yield four patch type samples per site and 216 samples from the 54 sites.

Seedling emergence experiments were conducted to determine the composition of the germinable soil seed bank (Thompson & Grime, 1979). The soil samples were sifted to remove coarse woody debris and thoroughly mixed. A 150 g sub-sample was taken and spread evenly (~ 5 mm deep) over sterilised sand in commercial germination trays (35 cm x 14 cm) and placed in an unheated greenhouse in Mildura, the south-western corner of the study area. The trays were watered regularly to keep the soil moist or at field capacity. The position of all trays was randomly allocated in order to account for a possible bias associated with tray position. Ten control trays, i.e. trays containing only sterilised sand, were evenly distributed in the greenhouse to control for glasshouse weeds and seeds within the sterilised sand. Emerging plants were counted and removed following identification, or representative samples re-potted to grow on to confirm sample identification. All emerging plants were removed before they could add further seeds to the samples. After a halt in germination, the soil in each tray was remixed in order to bring buried seed closer to the surface (Lunt, 1997). We acknowledge that some of the seeds in the soil seed bank may require specific dormancy cues. However, our comparison was based on the readily germinable fraction of the seed bank at each site. To account for warm season and cool season climatic cues, the seedling emergence experiment ran for an extended period from spring 2016 to late-autumn 2017 (242 days).

Data analyses

All identified species were assigned to three plant groups based on their; 1) origin (native, exotic); 2) longevity (annual, perennial) and 3) palatability (unpalatable, low palatability, high palatability)

using published information from Harden (1990), Cunningham, Mulham, Milthorpe & Leigh (1992) and other references (see Appendix S1). To test our first three hypotheses, we used general linear models (ANOVA) in R (Version 3.4.4, R Core Team, 2018) to assess the effects of three levels of site condition and four patch types on the richness and density of the germinable soil seed bank. Data were \log_{10} transformed prior to analysis to account for heteroscedasticity. The first stratum of the ANOVA model examined plant community effects (Red gum, Black box, and Cypress pine) and the second stratum site condition (good, average, and poor) and its interaction with community. The third stratum examined patch effects (tree, shrub, grass, and open) and the two- and three-way interactions with site condition and community. Fisher's LSD test was used to compare group means.

To assess species assemblage among patches and site condition, our third hypothesis, we constructed a matrix of species abundance by patch type and used this to calculate Bray-Curtis dissimilarity values among the four patch types at each site, using the Vegan package in R (Oksanen et al., 2019; R Core Team, 2018). This procedure was repeated for all sites. We then used one-way ANOVA with the lme4 package (Bates, Machler, Bolker, & Walker, 2015) within R (R Core Team, 2018) to test whether the average similarity among patches differed among the three condition classes. Significant differences in dissimilarity among patches within the three condition classes were examined using Fisher's Protected Least Significant Difference (LSD) test. If our hypothesis were upheld, we would expect that patches within poor condition sites would be more similar than patches within high condition sites.

Results

A total of 24,651 seedlings, representing 192 species from 45 families, emerged from the soil seed bank (Appendix S1). No plants emerged from the ten control trays. We recorded 104, 101 and 112 species from Black box, Cypress pine and Red gum communities, respectively. Overall, 38% of seedlings were exotic species, with small differences among communities (Black box: 32%, Cypress pine: 36%, Red gum: 46%). The germinable seed bank was dominated by forbs (73%), grasses (18%) and sedges (5%). Red gum had significantly greater densities of all plants, and native and perennial plants, than the remaining communities (Fig. 1; Appendix S2) and had the

greatest richness of all plants overall and all plant groups except exotic species (Fig. 2, Appendix S3).

Condition effects on seed banks

The only significant effect of condition on the seed bank was lower seed density of highly palatable plants at poor condition sites ($F_{2,12} = 4.26$, $P = 0.05$; Appendix S4). The richness of the seed bank did not vary with site condition for any plant trait group. We also found that the similarity in seed bank composition among patches did not change with site condition ($P = 0.26$), and these results were consistent among the three communities ($P = 0.46$; Fig. 3).

Effects of patch type on seed bank density and richness

Across all communities, patch type appeared to affect plant species according to their traits, and this was most obvious in the differences in seed densities (Fig. 1). Density of seeds of perennial plants was significantly lower in the open than under vegetated patches ($F_{3,135} = 3.13$, $P = 0.027$; Fig. 1), but there were no significant effects for annual plants. The densities of unpalatable plants and those of low palatability also varied among patch types, but there were no patch effects for highly palatable species. For unpalatable plants, seed density was lower under trees than the other patch types ($F_{3,135} = 4.02$, $P = 0.009$; Fig. 1; Appendix S2). For low palatability plants, however, seed density was lower in the open than the vegetated patches ($F_{3,135} = 4.82$, $P = 0.003$; Fig. 1). The density of native plants did not differ significantly among the four patch types ($P > 0.05$; Appendix S2). For exotic species however, seed density was greater under trees than the other patches in Cypress pine and Black box, but not in Red gum (Community x Patch interaction: $F_{6,135} = 2.15$, $P < 0.05$; Fig. 1). Despite these trait-specific results there was no overall effect of patch type on total seed density ($P > 0.05$; Appendix S2).

Plant origin and lifespan determined whether species richness varied among patches. Native plant richness was significantly greater in perennial patches than open patches ($F_{3,135} = 5.59$, $P < 0.001$; Appendix S3, Fig. 2), and perennial plant richness was significantly greater in vegetated patches than open patches ($F_{3,135} = 3.24$, $P = 0.024$; Fig. 2).

Discussion

Our results were generally consistent among communities, with only one community-level difference related to the density of exotic plants, providing little support for our first hypothesis. Similarly, we found only partial support for our second hypothesis, and no support for the third hypothesis, of a condition effect on the seed bank, with both a lower density of seeds of highly palatable plants at poor condition sites only, and no apparent effect of condition on seed bank heterogeneity among patch types. However, the richness and density of seeds from several trait groups varied with patch types (Hypotheses 4 and 5). Overall, our results suggest that patch type has a greater influence on the density and richness of the seed bank than site condition. Furthermore, the effect of patch type on the seed bank was dependent on plant traits and perennial plant patch identity (tree, shrub, grass).

269

Seed bank characteristics and site condition

Site condition in our study had no effect on richness, density or heterogeneity of the germinable seed bank of any trait group, except for a lower density of highly palatable species at poor condition sites. Declining site condition generally equates with a loss of disturbance-sensitive plant species (McIntyre & Lavorel, 1994; Yates, Norton & Hobbs, 2000; Eldridge et al., 2018) and often an increase in exotic richness (Wellstein, Otte & Waldhardt, 2007), but this was not the case in our seed-bank study. Mixed effects of site condition and livestock grazing on soil seed banks have been widely reported in the literature, with some studies reporting negligible differences between seed bank density or richness of heavily grazed and lightly grazed sites (Meissner & Facelli, 1999; Davies, Mackay, Whalen & Smyth, 2018), and others finding differences only under heavy grazing (Kinloch & Friedel, 2005; Navie, Cowley & Rogers, 1996) or increases in annual seed bank species with increasing disturbance (Snyman, 2004; Leder et al., 2017). These inconsistencies likely arise from the fact that seed banks can persist for extended periods (Thompson & Grime, 1979; Bertiller, 1992) allowing persistent species to buffer against the effect of disturbance (Grimes, 1981). The typically low concordance between species in the germinable seed bank and species in the standing vegetation is related to many factors such as time of sampling and soil seed bank resilience. The lack of differences among condition classes could be explained, in part, by legacy effects of past disturbances resulting in a seed bank that contains a complement of exotic species that may not be present in the standing vegetation. Even though a site might currently have low levels of disturbance and therefore be classified as being in good condition, it may still contain a seed bank that is reflective of a past condition state. Furthermore,

291 as some exotic species often have large and persistent seed banks, which can germinate quickly,
292 have vigorous seedling stages, and can outcompete perennial competitors, they can be present in
293 seed bank at good condition sites long after the initial disturbance (Fisher, Lonerangan, Dixon &
294 Veneklaas, 2009).

295
296 *Effects of patch type on seed bank richness depend on plant traits*

297 We found no consistent relationship between specific vegetation patches and seed bank richness or
298 density. Rather, patch effects varied with specific plant traits, and while perennial patches were
299 generally more likely to have seeds of most plant groups, there were still some patch-specific
300 effects. For example, tree patches supported a lower density of seeds of unpalatable plants, but a
301 greater density of seeds of plants of low palatability (Appendix S2). We found some support for
302 our fourth hypothesis, with the density of exotics and perennials, and plants that were unpalatable
303 and of low palatability, favouring perennial patches over interspaces. However annual plants did
304 not exhibit major differences in richness or seed density in response to perennial patches or
305 interspaces. Perennial plant patches are critical elements of dryland systems, providing niches for
306 invertebrates and microbes (Ochoa-Huesa et al., 2017), and sinks for water, seeds and nutrients
307 (Soriano, Sala, Perelman, 1994; Eldridge, Zaady, & Shachak, 2002). The density of native and
308 perennial plant seeds was significantly greater in all perennial patches than the open interspaces,
309 consistent with the large body of evidence from drylands elsewhere (e.g. Caballero et al., 2008;
310 Aguiar and Sala, 1994). Our data, however, also show evidence that the distribution of the seed
311 bank is more complex than a simple perennial patch-bare interspace dichotomy.

312
313 Perennial patch type and configuration likely affect seed bank structure through multiple processes
314 that influence seed dispersal, seedling establishment and plant production *via* competitive and
315 facultative interactions (Pugnaire and Lazaro, 2000) and, as our study suggests, structure seed
316 bank species according to plant traits. We found only one significant community by patch
317 interaction, suggesting that perennial patches generally have consistent effects on seed capture and
318 retention, at least in our target communities. We did find a greater density of exotic seeds under
319 trees in Cypress pine and Black box communities than in the Red gum community (Fig. 1). This
320 may be partly explained by a combination of dispersal and facilitation mechanisms. A large
321 proportion of the exotic species we found in the seed bank of tree patches were wind dispersed and
322 are therefore more readily trapped by litter and debris found under trees. Tree patches are also

323 typically nutrient enriched, shaded environments (Manning, Fischer & Lindenmayer, 2006;
324 Howard et al., 2012), which have the potential to facilitate or 'nurse' exotic species that are adapted
325 to high nutrient and less hostile environments. Many exotic species that are prolific seeders (e.g.
326 *Sisymbrium*, *Brassica*, *Psilocaulon* spp.) tend to persist within perennial patches long after the
327 removal of any disturbances that lead to their establishment (Soliveres, Moneris, & Corina, 2012;
328 Rolhauser et al., 2013).

329
330 The greater density of perennial plant seeds in perennial patches may result from differences in
331 seed morphology. Perennial species typically have relatively large seeds that produce larger
332 seedlings that can more readily compete with established vegetation within a perennial plant patch
333 (Jakobsson & Eriksson, 2000). In contrast, annual species are generally short statured with small
334 seeds (Moles, Falster, Leishman & Westoby, 2004) but compensate by producing more seeds that
335 disperse further and are trapped more easily, even in open areas. However, their successful
336 establishment rate is low, even within perennial patches (Farrell et al., 2012). Seed dispersal
337 mechanisms also affect seed densities across the landscape. Perennial herbs often establish a short
338 distance from their parent, within their parents' associated patch, and this short dispersal trait tends
339 to intensify as plants become more tolerant of arid conditions ('seed source effect'; Chambers &
340 McMahon, 1994). The seeds of annual species, however, disperse larger distances and might
341 therefore have a more uniform distribution within the landscape. Competitive interactions and
342 environmental conditions also contribute to affect plant species establishment (Rolhauser et al.,
343 2013).

344
345 We found only one significant community by patch interaction, showing greater density of exotic
346 seeds under trees in Cypress pine and Black box communities than in the Red gum community
347 (Fig. 2). Functionally, our three communities differ in the relative influence of aeolian and fluvial
348 processes that are known to affect seed dispersal mechanisms (Hintze et al., 2013). Intermittent
349 flooding in the Red gum, and to a lesser extent, Black box communities, likely removes litter and
350 soil material from around the base of trees, shrubs and perennial grasses, altering the distribution
351 of seeds (Colloff & Baldwin, 2010) and leading to the regular turnover of seeds (Bourgeois,
352 Boutin, Vanasse & Poulin, 2017). Tree size and canopy cover also increase from Cypress pine to
353 Red gum. Given that perennial patches influence the zone beyond their canopies (Caballero et al.,
354 2008; Maestre & Cortina 2005), seed banks from more open areas in Red gum, and to a lesser

355 extent, Black box communities, may be influenced by the spatial architecture of surrounding
356 patches. For example, seed deposition is higher on bare surfaces on the leeward side of perennial
357 shrubs or trees due to gradients in wind movement (Caballero et al., 2008). The deep cracking
358 clays in Black box and Red gum could also provide surface microtopography that regulates seed
359 dispersal and colonisation by trapping seeds in relatively open areas (Boeken & Shachak, 1994).
360 These functional processes may also further explain our results for the density of exotic plant
361 seeds and seeds of low palatability plants, where the seed bank of the interspaces did not differ
362 from those in grass or shrub patches.

363
364 Land management practices such as livestock grazing and vegetation removal, and natural
365 processes such as woody encroachment, can alter the cover and spatial arrangement of perennial
366 patches, and have the potential to alter the composition of the future biotic community. These
367 practices also come with their own inherent processes that further alter species persistence and site
368 resilience. For example, grazing is known to reduce palatable species in the above-ground plant
369 community (Lunt, Eldridge, Morgan & Witt, 2007) and this can alter the composition (Leder et al.,
370 2017; Sanou, Zida, Savadogo & Thiombiano, 2018), and density (Kinloch & Friedel, 2005) of the
371 seed bank, and reduce the relative cover of perennial patches that retain seeds (Tongway et al.,
372 2003). Other processes are known to affect landscape-level seed distribution such as the foraging
373 activities of animals, particularly ants and rodents (Reichman, 1984), and seed dispersal by
374 perching birds or rodents (Herrera & Garcia 2009). Faunal activity that disperses seeds is
375 encouraged by perennial vegetation which further enhances the positive effects of vegetation
376 patches in the landscape.

377 378 **Conclusions**

379
380 Perennial patches can affect seed bank structure by affecting seedling germination and
381 establishment, and subsequent seed dispersal, and as our study suggests, can affect species
382 assemblages depending on plant traits. Our study reinforces the notion that perennial patches play
383 significant roles in maintaining the richness and density of the soil seed bank. Despite
384 considerable disturbance, lower soil health and lower above-ground vegetation cover, our seed
385 bank study indicated that the germinable seed bank was relatively resilient to reductions in site
386 condition, with poor condition sites even containing rare plants and species missing from the

above-ground vegetation. Thus low quality sites may still have positive conservation values and respond to restoration actions such as grazing removal as long as the perennial patches, and their attendant seed banks, remain largely intact. This has important implications for land managers aiming to restore functional productive ecosystems, and reinforces the need to maintain patches in the landscape as refugia for seeds. The management of exotic species, however, is likely to be an ongoing management problem given their persistence in sites of good condition. Overall, our study finds that the restoration of degraded woodland sites will be facilitated by retaining and enhancing perennial plant patches because these are critical structural elements in woodland systems that sustain plant communities and buffer against future disturbance under a changing climate.

397

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399

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405

406 **Authors' contributions**

407

J.V., D.J.E., I.O., and S.K.T. conceived and designed the study; J.V., D.J.E., and S.K.T. collected the field data; J.V. conducted the seedling emergence experiments; D.J.E. and J.V. analysed the data; J.V. led the writing of the manuscript, and all authors contributed critically to the drafts and gave final approval for publication.

412

413 **DATA ACCESSIBILITY**

414

Data on seed density and abundance will be made publicly available in Figshare
<https://10.6084/m9.figshare.11752695>

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634

635 SUPPORTING INFORMATION

636 Additional supporting information may be found online in the Supporting Information section.

637

638 **Appendix S1.** Vascular plant species recorded during the seedling emergent experiment.
639 **Appendix S2.** Influence of community, patch type and site condition on the density of germinable
640 seeds.
641 **Appendix S3.** Influence of community, patch type and site on the richness of the germinable soil
642 seed bank.
643 **Appendix S4.** Influence of site condition on the density (seeds m⁻²) and richness of the
644 germinable soil seed bank.
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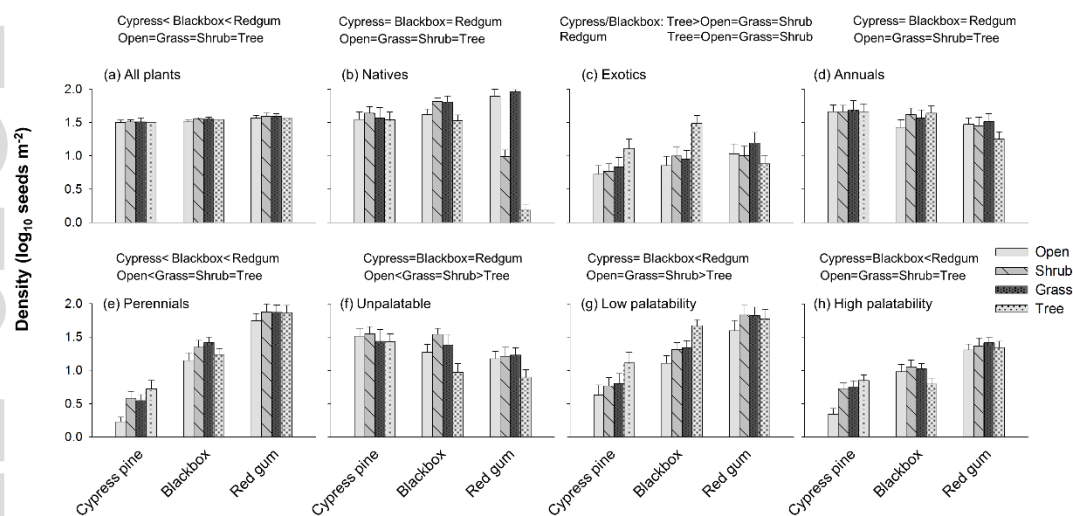


Figure 1. Mean (+ SE) density of seeds (seeds m⁻², log₁₀ scale) of all plants, natives, exotics, annuals, perennial, unpalatable, low palatability and high palatability. in relation to vegetation community and patch type. The main effects for Community and Patch type are presented in each figure. For Exotics, there was one significant Community by Patch interaction.

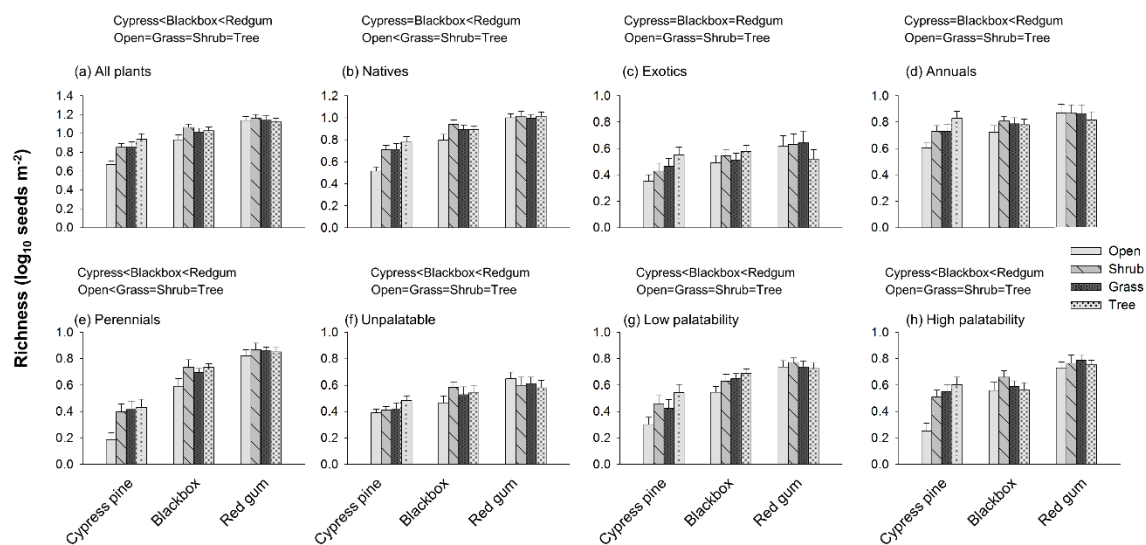


Figure 2. Mean (+ SE) richness of seeds (log₁₀ scale) of all plants, natives, exotics, annuals, perennial, unpalatable, low palatability and high palatability. in relation to vegetation community and patch type. The main effects for Community and Patch type are presented in each figure. There were no significant Community by Patch type interactions for richness.

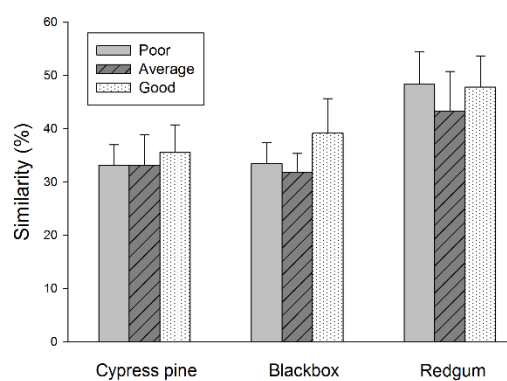


Figure 3. Mean (+ SE) percentage similarity (Bray-Curtis) among communities and condition classes. There were no significant Community, Condition class, nor Condition by Community interactions.