

## UN DECADE ON ECOSYSTEM RESTORATION

## Research Article

# Recovery of woody but not herbaceous native flora 10 years post old-field restoration

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**Funding information**

Department of Education, Skills and Employment, Australian Government; Bush Heritage Australia; Department of Agriculture, Water and the Environment; Carbon Neutral Pty Ltd

Handling Editor: Ji-Zhong Wan

**Abstract**

1. Vegetation recovery in old fields towards mature reference states is often limited by abiotic and biotic thresholds resulting from agricultural land use legacies, as commonly highlighted using state and transition models. Old-field restoration may include interventions (e.g. planting of vegetation) to overcome these thresholds and assist transition between states. However, our understanding of the effectiveness of these interventions is limited.
2. Using a point-intercept transect method, we surveyed nine sites, each comprising a triplet of fallow cropland, planted old field and woodland reference plots to reflect states of old-field restoration, from the degraded state to the reference state. We compared ground cover attributes, and richness and cover of woody and herbaceous flora species, using ANOVA and multivariate analyses.
3. We found that a decade after planting, cover of leaf litter and woody debris in planted old fields were significantly higher than in the fallow croplands; however, woodland reference conditions were not achieved. Cover of logs was similar to the fallow cropland. Woody species cover and richness were similar in planted old fields and woodland reference plots, with planted old fields having more than 60% of the shrub species richness and cover, and similar tree species richness, to the woodland reference plot.
4. In contrast, whilst herbaceous species contributed more than half the plant species richness in reference woodland plots, there were significantly fewer herbaceous species in the planted old fields, which were more similar to the fallow croplands. Cover of exotic annual forbs in planted old fields was about half that of fallow cropland, and exotic annual grass cover was similar to the reference woodland.
5. Our results show that active restoration of old fields increased leaf litter, woody debris and cover and richness of trees and perennial shrubs. However, native herbaceous species richness, and to some extent cover, remained similar to the fallow cropland. To effect transitioning of the herbaceous layer to the woodland reference state, further intervention such as removal of exotics, followed by sowing or planting native herbaceous species, may be necessary.

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## KEYWORDS

agricultural legacies, herbaceous species, leaf litter, native grasses, old-field restoration, semi-arid woodland, state and transition models, woody debris

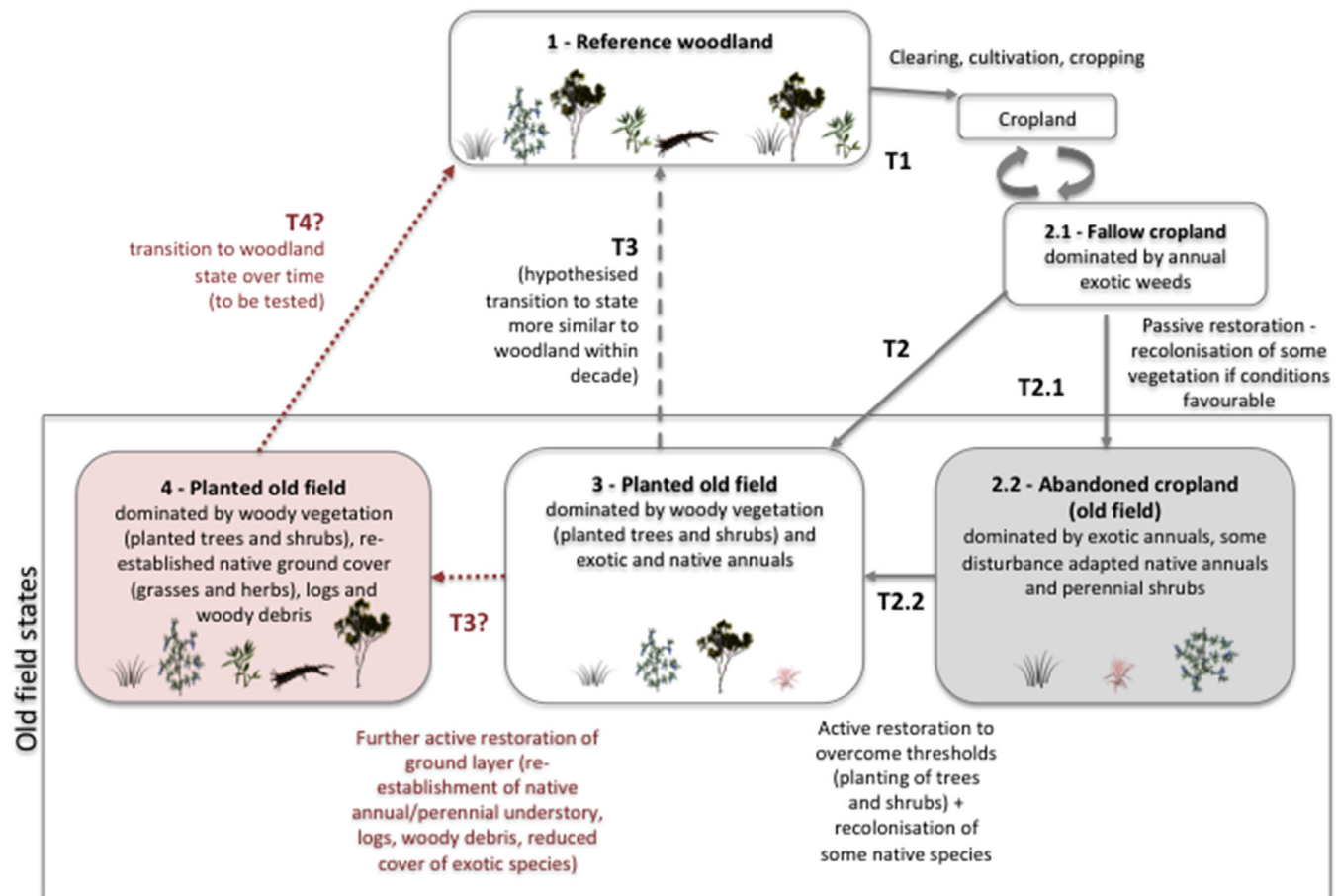
## 1 | INTRODUCTION

Restoration of the world's old fields has challenged restoration practitioners and ecologists for decades (Hobbs, 2012; Queiroz et al., 2014). Key ecological challenges in old-field restoration are understanding and overcoming abiotic and biotic thresholds that limit recovery (Cramer et al., 2008). Old fields have been difficult to restore due to the extensive modification of soil properties and vegetation communities following cultivation, and the resulting degradation of these key ecosystem components (Cuesta et al., 2012; de la Pena et al., 2016; Morris et al., 2013). Interventions are often needed to assist or accelerate the development of vegetation and the transitioning between vegetation states (Funk et al., 2008; Hobbs, 2012; Lavorel et al., 1999).

State and transition models describing vegetation states and potential thresholds that prevent transitions between states (Bestelmeyer

et al., 2017; Westoby et al., 1989) assist restoration ecologists and practitioners in the prediction of drivers of change and the interventions needed to overcome thresholds (Suding & Hobbs, 2009). These models can incorporate hybrid states (i.e. mixes of native and exotic plant species [Hobbs et al., 2009]) and alternative stable states (i.e. stuck states [May, 1977]), which are relevant to old-field restoration (Figure 1) (Rumpff et al., 2011; Standish et al., 2008, 2009).

In agricultural landscapes, vegetation development and transition between old field states is dependent on the extent of agricultural legacies, climate and vegetation type (Cramer et al., 2008; Flinn & Marks, 2007; Standish et al., 2007). Where agriculture used traditional farming practices, including minor soil alteration, and in landscapes with large areas of intact native vegetation to facilitate seed dispersal, vegetation can assemble and develop between vegetation states to reach a community similar to the historic reference state after abandonment



**FIGURE 1** State and transition framework for old-field restoration. Vegetation states (boxes) and transitions between them (T1 to T4) are described. States 1, 2.1 and 3 are explored in this study, State 2.2 (grey) is defined based on prior research (e.g. Standish et al., 2008) and transition to woodland state through additional restoration action (red) is proposed for future research

and without intervention (Cramer et al., 2008; Flinn & Marks, 2007). However, as the land use legacies from agriculture intensify, modification of soil properties increases, abiotic and biotic thresholds are more likely, and the probability of community re-assembly is reduced, to the point where old fields remain in a depauperate state, with little or no recovery towards a reference state (Brudvig et al., 2013; Cramer et al., 2008).

Research on old-field restoration to native eucalypt woodlands and woody shrublands in semi-arid Western Australia has indicated that native vegetation on old fields does not recover to reference state, even decades after abandonment, due to abiotic and biotic thresholds (Standish et al., 2006). Whilst a few opportunistic native species (e.g. *Salsola australis*, *Maireana brevifolia*, *Ptilotus polystachyus*) may establish at the site through wind or ant dispersed seeds (Harris & Standish, 2008; Standish et al., 2007), recovery of the species composition of the reference vegetation community is not achieved (Arnold et al., 1999) (Figure 1, State 2.2). In particular, elevated soil nutrients (e.g. phosphorus) and limited native seed availability due to depauperate soil seed banks, limited seed dispersal, seed and seedling predation (e.g. ants and agricultural pests) coupled with overabundant exotic seed banks pose substantial barriers to recovery (Standish et al., 2008; Standish et al., 2006; Standish et al., 2007; Woodall, 2010). Additionally, elevated soil nutrient concentrations, in particular plant available phosphorus (P) and nitrogen, provide favourable conditions for agricultural weeds, which tend to persist on old fields. Native plants, in particular those adapted to low nutrient soils (e.g. in old landscapes of Western Australia, but also South Africa, Brazil [Lambers et al., 2010]) may fail to re-establish due to nutrient-enriched soils and competition with exotic species (Lambers et al., 2013; Prober & Lunt, 2009).

Because of the time lag associated with woody vegetation establishment, ground cover attributes such as leaf litter, woody debris and larger fallen timber can be slow to recover or missing altogether (Vesk, Mac Nally, et al., 2008; Vesk, Nolan, et al., 2008). Fewer studies focus on these attributes, despite being important for nutrient cycling, reestablishment of soil organic matter and soil carbon, improvement of soil condition, plant–soil feedbacks and fauna resources (habitat, food) (Bowman & Facelli, 2013; Manning et al., 2013; Wardle et al., 2004). Therefore, there is a need to measure ground cover attributes in studies of old field recovery and restoration.

In woody ecosystems where recovery is seldom achieved through passive restoration (i.e. vegetation development following abandonment), active restoration measures such as direct seeding or planting of seedlings coupled with scalping and weed control are often applied. These measures return a subset of the native reference vegetation and may facilitate transition to a hybrid vegetation state (Suding et al., 2004) (Figure 1). Active restoration tends to focus on the establishment of woody native species, because these provide structure, and because seeds and methods of propagation and establishment are readily available. Herbaceous native species are less commonly included in the restoration species mix, as they can be difficult to source and may not establish in competition with invasive agricultural weeds (Smallbone et al., 2008). The assumption is that woody species,

once established, might facilitate return of herbaceous species. However, tests of this assumption are rare.

This study focuses on York gum woodlands, dominated by *Eucalyptus loxophleba* overstory, a vegetation community that was once widespread across the study region, but due to extensive clearing for agriculture, it is now listed as threatened (Department of the Environment, 2020). We measured plant community attributes, including woody debris and leaf litter in nine sites that included triplets of fallow cropland (initial state indicating the starting point of restoration), planted old fields (transitioned state achieved through intervention) and reference woodlands (desired end state). We coupled these data with soil properties (reported in Parkhurst et al., 2021) to test for presence of abiotic thresholds. Using a state and transition model (Figure 1) as a framework for our research, we hypothesized that, a decade after cessation of cropping and planting of key native woody species:

1. Native plant species richness and cover on planted old fields would increase, compared with fallow cropland, and to levels similar to that in woodland reference plots through a combination of plantings and species recolonising from nearby remnants.
2. Ground cover attributes (leaf litter, woody debris, logs) on planted old fields would be greater than fallow cropland and approach levels in woodland reference plots, with the exception of logs, which would not appear within a decade (i.e. may take centuries).
3. Exotic species would persist and dominate the vegetation cover of planted old field plots similar to fallow croplands, due to abiotic and biotic thresholds (i.e. elevated soil nutrients, in particular soil P, and competitive weed species dominating soil seed banks).

## 2 | MATERIALS AND METHODS

### 2.1 | Study location

The study was conducted in the northern wheatbelt of south-western Australia (Lat  $-29.66^\circ$ , Long  $116.18^\circ$ ), a region dominated by agriculture (cropping and grazing). The climate is Mediterranean to semi-arid, with predominant winter rainfall, although rainfall is highly variable across years (Hobbs, 1993). Across the study sites, long-term mean annual rainfall ranged from 336 to 343 mm and mean monthly maximum temperatures ranged from  $18.0^\circ\text{C}$  (July) to  $37.4^\circ\text{C}$  (January) (Bureau of Meteorology, 2020). Annual rainfall during restoration years ranged from 236 to 438 mm with mean monthly maximum temperatures of  $17.1^\circ\text{C}$  (July) to  $39.5^\circ\text{C}$  (January) (Bureau of Meteorology, 2020). Clearing of native vegetation for mixed farming began in the 1900s and continues to date, with the remaining 10% typically occurring in small and highly fragmented patches (Hobbs, 1993).

Soils are ancient and infertile, in particular P deficient, which is typical for landscapes without recent disturbances such as glaciation or volcanic eruptions (Lambers, 2014). The rocks that form the substrate for the soils of the region are up to 2900 million years old; these have weathered over geological time to produce a mantle of sandy and lateritic soils underlain by mottled and pallid zones of weathered



**FIGURE 2** Example vegetation states: Fallow cropland, planted old field and woodland reference

materials art (McArthur, 1991). Prior to clearing for agriculture, woodlands were expansive and were dominated by *Eucalyptus loxophleba* Benth. and *Acacia acuminata* Benth. (Anand & Paine, 2002; Lambers, 2014; McArthur, 1991). Understorey vegetation is composed of a highly diverse annual and perennial forb layer, with sparse perennial grasses (e.g. *Austrostipa* spp.) and succulent shrub species (e.g. *Maireana* spp., *Atriplex* spp.). More details on the study location including a map can be found in Parkhurst et al. (2021).

## 2.2 | Study site selection and sampling design

We selected nine study sites, each incorporating three vegetation states (Figure 2): (a) fallow cropland, representing the restoration starting point, (b) planted old field (actively restored site) and (c) reference York gum (*E. loxophleba*) woodland, as the desired end state. Sites were selected based on (1) best available reference state representative of the historical reference state, and (2) best match to soil type, topographic position and rainfall within each triplet. The reference woodlands had little or no weed cover and grazing history. York gum was dominant on all planted old fields (Figure 2). On average, five ( $\pm 1.1$ ) woody species, commonly occurring in woodlands, were planted on old fields with 2–6 m between planting rows (Table S1). Planted old fields were between 8 and 13 years old at time of sampling, and distance from remnant vegetation averaged 279 m ( $\pm 162$  m) (Table S1). Restoration aims included recovery of biodiversity, provision of fauna habitat and/or ecosystem services (i.e. carbon sequestration) (further details in Parkhurst et al., 2021). Plots in fallow cropland were established where cropping and/or grazing had not occurred for 1–3 years. All plots were placed at least 10 m from any edge habitat. Plots measured 20 m  $\times$  50 m and were marked with posts at each corner prior to data collection.

## 2.3 | Plant species richness and cover

All annual and perennial plant species were recorded in spring 2017 within each plot and identified to genus and species level where possible. Nomenclatures follow the Western Australian Herbarium (2017).

A point intercept method previously demonstrated to provide objective and repeatable measures of cover (Godínez-Alvarez et al., 2009; Prober et al., 2011) was used to quantify cover of individual plant species, total vegetation cover and substrate types (i.e. bare ground, litter cover, plant cover). Ground cover, individual species, and canopy cover intercepting at every 2 m along four parallel, evenly spaced 50 m transects across each plot were recorded using a vertically placed dowel (8 mm wide, 2 m tall), resulting in 100 intercepting points per plot. For planted old fields, transects were placed parallel to planting rows, with two centred on rows and two centred between rows. This approximately represented the relative abundance of planted rows and non-planted inter-rows. If a species was recorded in the plot but did not intercept the dowel on any transect, it was assigned 0.5 points. This method provided a measure of relative abundance (percentage cover) of plant species across the plot and is subsequently referred to as cover.

To calculate species richness and cover across different life history and growth forms, species were classified into the following groups: total, native trees, native shrubs, native non-planted shrubs, native grasses, native perennial forbs, native annual forbs, exotic grasses and exotic annual forbs using the Western Australian Herbarium (2017) classification (Table S4).

## 2.4 | Woody debris and leaf litter surveys

Leaf litter dry mass was estimated by collecting leaf litter (loose woody leaves) from five randomly placed 25 cm  $\times$  25 cm quadrats along two 50-m transects across each plot. Litter was stored in paper bags for transportation and then oven dried for 36 h at 60°C. The dried litter was weighed to three decimal points. Cover of fine and coarse woody debris and litter depth was estimated at every meter along two 20-m transects for each plot. Woody debris was classified by diameter (<3 cm, 3–5 cm, 5–10 cm, 10–20 cm, >20 cm). Length, max and min diameter was measured for all logs with a diameter greater than 10 cm. These observations were used to calculate the relative volume (m<sup>3</sup>) of fallen woody debris for each plot. Decay state was also recorded and classified based on a visual scale of log decay: 0 = no obvious decay to 5 = mostly decayed to particulate matter.

## 2.5 | Data analysis

Vegetation cover and richness data were analysed using a two-way ANOVA according to the Randomized Complete Block Design, with vegetation state as the treatment (fixed effect) and study site as the block (random effect) (R *stats* package, R version 3.6.1 [R Core Team, 2019]). Data were log transformed where appropriate. If transformations did not achieve normality and homogeneity of variance, we applied non-parametric tests (Kruskal–Wallis). Vegetation cover data were used to produce a compact ordered community table using the ‘vegemite’ function, and Shannon and Simpson diversity indices were calculated for flora species using the *diversity* function in the *vegan* package in R (Oksanen et al., 2007). We used linear regression analyses to test for the effects of vegetation age and distance from nearest remnant on vegetation cover attributes for all planted old field plots (function *lm*, in the *stats* package in R). We found no statistically significant correlation between any of the vegetation cover and species richness response variables and restoration age or distance from nearest remnant (Table S1), therefore we did not include these data in final analyses.

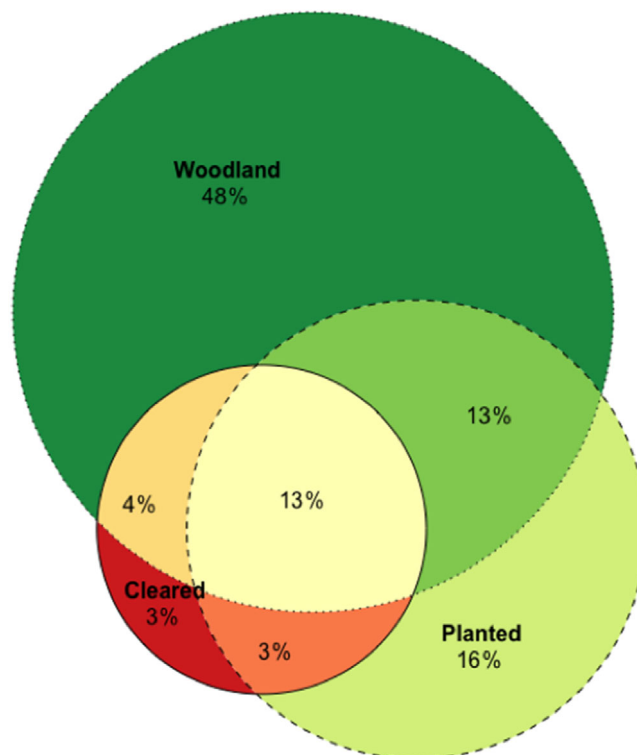
We used non-metric multidimensional scaling (nMDS) analyses, and vector correlation applying the ‘metaMDS’ functions (*vegan* package in R), to assess differences in plant composition across fallow cropland, planted old fields and woodland reference plots. Dissimilarities were calculated using the Bray–Curtis index (Bray & Curtis, 1957). We fitted grouping and explanatory variables (richness and cover of functional groups, and soil chemistry, respectively) to the nMDS, using the function ‘envfit’ (*vegan* package in R), to test how these variables independently correlated to the unconstrained ordination. Significance ( $p < 0.05$ ) of the variables was assessed using permutation tests. Ordination scores were also used to order the compact community table to better understand species contribution to differentiation among states. We use the R package ‘*mvabund*’ (Wang et al., 2012) to test for difference in community composition across the three states. We generated area-proportional Euler diagrams for the number of exclusive and shared native or exotic species between fallow croplands, planted old fields and reference woodlands using the ‘euler’ function in the *eulerr* package in R (Larsson et al., 2016).

## 3 | RESULTS

### 3.1 | Ground cover attributes

On average, planted old fields had higher ground cover than the fallow croplands (Table 1). However, reference woodland conditions were not achieved approximately 10 years after planting (Table 1). Rather, woody debris cover and leaf litter cover, biomass and depth in planted old fields were transitioning towards reference woodland conditions; woody debris reached 35% of the reference woodland plot cover, and leaf litter cover, biomass and depth were at approximately 70% of the levels in reference woodland (Table 1). In contrast, there were significantly fewer and smaller logs in the planted old fields than the refer-

## Native Plant Species Richness



**FIGURE 3** Euler diagram for shared and exclusive native species in fallow croplands, planted old fields and woodland reference plots. There were 159 native species total across all plots

ence woodlands, as might be expected for young plantings (Table 1). No logs were recorded in the fallow croplands and only two were present in one planted old field (site 10, which was the oldest restoration site). A total of 47 logs were recorded in the reference woodlands ( $4.7 \text{ mean} \pm 0.47$ ); of these, 19% were classified as being in decay state 3, and 81% in decay state 4. Total bare ground was highest in the planted old field, and significantly higher than in the fallow cropland and the reference woodland plots (Table 1).

### 3.2 | Flora species richness and cover

We recorded a total of 198 plant species across all treatments, of which 159 were native and 42 were exotic species (Table S3). Overall, native plant species richness was highest in the woodland reference plots, with 48% of native species only occurring in these plots (Figure 3). In contrast, the planted old field plots had fewer native species, with only 16% being unique to the planted plots, sharing 13% with the woodland reference and 3% with the fallow cropland (Figure 3). The fallow cropland state had the lowest native species richness, with 3% unique species, 3% shared with the planted old fields and 4% shared with the woodland reference. Only 13% of native species were shared between all three vegetation states (Figure 3). ANOVA results supported these trends, showing that total native species richness on planted old fields

**TABLE 1** Mean vegetation attributes at sampling plots (1 SE,  $n = 9$ ). Different letters represent significant differences between treatments

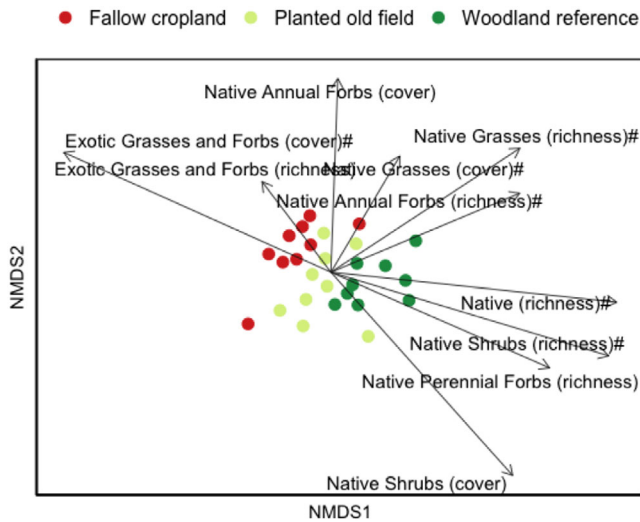
Variable	Unit	<i>p</i>	Fallow cropland	Planted old field	Woodland reference
<i>Ground cover</i>					
Bare ground	% points	<0.01	26.67 ± 5.1a	44.00 ± 4.9b	32.44 ± 3.2a
Woody debris	% points	<0.001	0.11 ± 0.1a	6.00 ± 1.3b	16.67 ± 2.3c
Leaf litter (cover)	% points	<0.001	0.00 ± 0.0a	33.11 ± 4.1b	46.44 ± 1.6c
Leaf litter (biomass)	g (dry weight)	<0.001	0.00 ± 0.0a	8.62 ± 1.7b	13.78 ± 0.9c
Leaf litter (depth)	cm	<0.001	0.00 ± 0.0a	0.55 ± 0.1b	0.68 ± 0.1c
Logs (>10 cm diameter)	% points	<0.001	0.00 ± 0.0a	0.22 ± 0.2a	8.0 ± 1.0b
Logs (>10 cm diameter)	Volume	<0.001	0.00 ± 0.0a	0.003 ± 0.003b	0.18 ± 0.1c
Logs (>10 cm diameter)	m	<0.001	0.00 ± 0.0a	0.26 ± 0.3b	3.76 ± 0.5c
<i>Native species cover</i>					
Trees	% points	<0.001	0.00 ± 0.0a	28.67 ± 4.9b	45.56 ± 6.0c
Shrubs total	% points	<0.001	2.89 ± 2.0a	17.5 ± 3.7b	29.78 ± 5.1b
Non-planted shrubs	% points	<0.001	2.89 ± 2.0a	9.06 ± 3.5a	29.78 ± 5.1b
Grasses	% points	0.145	3.11 ± 1.3	5.83 ± 3.4	7.44 ± 2.2
Perennial forbs	% points	<0.05	0.39 ± 0.1a	1.11 ± 0.4ab	5.88 ± 2.3b
Annual forbs	% points	0.09	12.33 ± 4.2	3.72 ± 1.4	7.28 ± 2.0
<i>Exotic species cover</i>					
Grasses	% points	<0.001	37.2 ± 8.7b	7.6 ± 2.0a	2.39 ± 0.5a
Annual forbs	% points	<0.05	32.72 ± 8.3b	16.28 ± 4.5ab	3.72 ± 0.9a
<i>Species richness</i>					
Total species richness	Count	<0.01	16.66 ± 2.1a	24.55 ± 3.6ab	35.11 ± 3.8b
<i>Native species richness</i>					
Total	Count	<0.001	8.00 ± 1.5a	15.22 ± 2.4b	27.11 ± 2.8c
Trees	Count	<0.001	0.00 ± 0.0a	1.66 ± 0.3b	1.44 ± 0.3b
Shrubs total	Count	<0.001	1.77 ± 0.4a	6.77 ± 1.3b	10.22 ± 1.4b
Non-planted shrubs	Count	<0.001	1.77 ± 0.4a	4.22 ± 0.7a	10.22 ± 1.4b
Grasses	Count	<0.05	1.88 ± 0.5a	1.88 ± 0.5a	3.33 ± 0.4b
Perennial forbs	Count	<0.001	0.89 ± 0.3a	1.67 ± 0.6a	4.33 ± 0.6b
Annual forbs	Count	<0.001	3.44 ± 0.8a	3.22 ± 0.9a	7.78 ± 1.3b
<i>Exotic species richness</i>					
Total	Count	0.767	8.66 ± 1.2	9.33 ± 1.8	8.00 ± 1.5
Grasses	Count	0.81	3.78 ± 0.7	3.56 ± 0.7	3.44 ± 0.5
Annual forbs	Count	0.669	4.89 ± 0.7	5.78 ± 1.2	4.56 ± 1.1
<i>Diversity indices</i>					
Shannon-wiener diversity index	Native species	<0.01	1.46 ± 0.3a	1.81 ± 0.3ab	2.49 ± 0.1b
Simpsons diversity index	Native species	0.07	0.61 ± 0.1	0.72 ± 0.1	0.86 ± 0.0

P values in bold indicate statistical significance of  $p < 0.05$ .

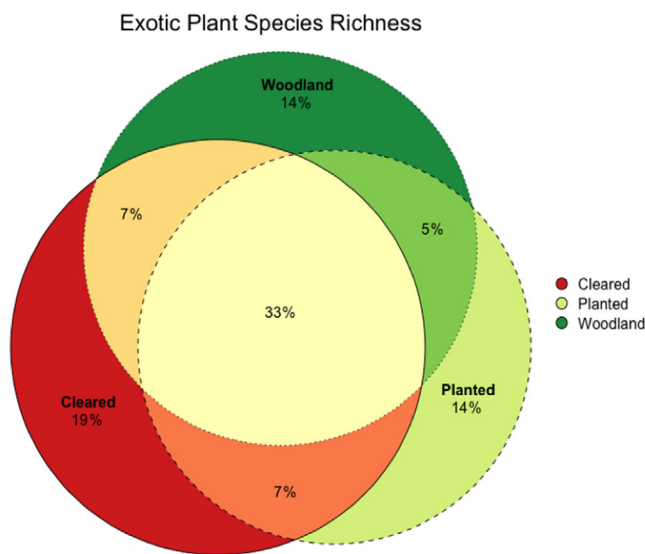
was significantly higher than fallow cropland, but did not reach woodland reference conditions (Table 1). Species diversity indices (Shannon Wiener and Simpson's) showed highest diversity in the woodland reference plots; however, these were not significantly different to the planted old field plots (Table 1).

At a plant functional group level, species richness of shrubs and trees in planted old fields was similar to the reference woodlands, which have few tree species (<2) (Table 1; Figure 4). Planted old fields

supported woody shrub cover similar to the reference woodland state, but tree cover was significantly lower due to smaller tree crowns of young trees rather than low tree densities (Table 1). In contrast, whilst herbaceous species richness made up more than half of the total richness in the woodland reference state, richness of native grasses and forbs in planted old fields was more similar to the fallow cropland (Table 1). In particular, native perennial forb species on planted old fields showed no significant increase in cover or richness than the



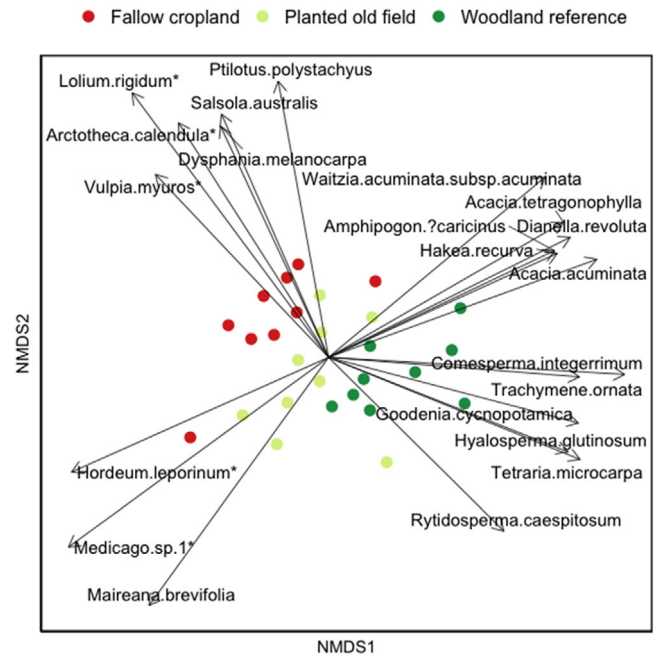
**FIGURE 4** Non-metric multidimensional scaling (nMDS) analysis of vegetation cover data, showing correlation of species functional groups. Vector length indicates the strength of the correlation. Significant vectors ( $p < 0.05$ ) are indicated with #



**FIGURE 5** Euler diagram for shared and exclusive exotic species in fallow croplands, planted old fields and woodland reference plots. There were 42 exotic species across all plots

fallow cropland (Table 1). Furthermore, native annual forbs and native perennial grasses showed no significant increase in species richness, although were present in similar cover across all vegetation states (Table 1).

Exotic plant species richness was highest in the fallow cropland, with 19% of species only found in the fallow cropland plots. In both woodland reference and planted old fields, 14% of the exotic species were unique. A total of 33% of exotic species were shared between all three states (Figure 5). Exotic grass cover was significantly and substantially higher on the fallow cropland than on the planted old field and woodland reference states (Table 1). Cover of exotic annual forbs was also

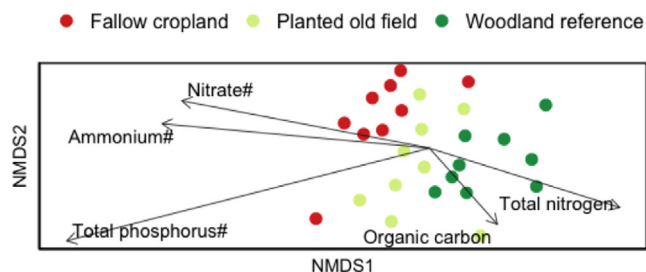


**FIGURE 6** Non-metric multidimensional scaling (nMDS) analysis of vegetation cover data, showing correlation of significant indicator species vectors ( $p < 0.05$ ). Vector length indicates the strength of the significant correlation. Exotics are indicated with asterisk (\*)

significantly higher on fallow croplands, when compared to the woodland reference state (Table 1). Exotic annual forb cover in planted old fields was about half that of fallow croplands, and more than four times higher than the woodland reference; however, the differences were not statistically significant (Table 1).

The patterns in floristic cover and diversity were reflected in clear separation among plot types on the ordination, with planted old fields intermediate between fallow cropland and reference woodlands (noting trees excluded) (Figures 4 and 6). Analysis of multivariate cover data showed a significant difference in species composition across the three states (likelihood-ratio test [LRT] = 365,  $p < 0.001$ ). Further investigation of the difference in exotic and native forb and grass cover between planted rows and inter-rows within planted plots did not reveal any significant differences (Table S2). A biplot overlay of soil chemistry data onto ordination of plant species assemblages revealed clear correlation of higher concentrations of nitrate and ammonium in the fallow cropland plots, as well as higher soil P in planted old fields and fallow croplands than reference woodlands (Figure 7, see also Parkhurst, Standish & Prober, 2021). In contrast, reference woodlands were characterized by high concentrations of organic carbon and total nitrogen (Figure 7).

All trees that had established on the old fields were planted, whereas 50% of total shrub species in the old field recolonized without assistance. Chenopods were the most common shrubs to colonize the planted old fields, including *Maireana brevifolia*, *M. tomentosa*, *M. planifolia*, *Salsola australis* and *Enchylaena tomentosa* (Figure 6; Table S1). Native species almost unique to reference woodlands included annual forbs (*Trachymene ornata*, *Hyalosperma glutinosum*), native grasses



**FIGURE 7** Non-metric multidimensional scaling (nMDS) analysis of vegetation cover data, showing correlation of soil chemical variables. Vector length indicates the strength of the correlation. Significant vectors ( $p < 0.05$ ) are indicated with #

(*Austrostipa nitida*, *A. elegantissima*) and other species typically found in York gum woodlands (e.g. *Dianella revoluta*, *Comesperma integerrimum*, *Rhagodia* sp. *Watheroo*). Species more prominent in fallow croplands included exotic annual grasses (*Hordeum leporinum*, *Lolium rigidum*, *Lamarckia aurea*) and several exotic annual forbs (e.g. *Medicago* sp., *Sisymbrium orientale*, *Spergula arvensis*, *Mesembryanthemum nodiflorum*), as well as opportunistic native annual forbs (*Ptilotus polystachyus*, *Dysphania melanocarpa*, *Atriplex codonocarpa*) and the short-lived shrub *Salsola australis* (Figure 6; Table S1).

#### 4 | DISCUSSION

Our first hypothesis, stating that native plant species richness and cover would increase to levels similar to the woodland reference in response to active restoration was partially supported. In particular, results suggested that planting of native woody species facilitated transition from a fallow cropland to a planted old field dominated by woody vegetation similar in richness/composition to the reference woodland (Figure 1, State 3).

The increase in tree species richness and cover was achieved by planting, though shrub species richness and cover improved due to planting coupled with recruitment of other species (e.g. *Maireana brevifolia*, *M. tomentosa*, *M. planifolia*, *Salsola australis* and *Enchylaena tomentosa*). Most of these volunteer shrubs are chenopods, commonly found in semi-arid woodlands (McArthur, 1991), indicating vegetation development towards the woodland reference rather than a switch to a new state (Figure 1). Various traits may have assisted re-establishment including dispersal traits. *Maireana* species have winged seeds well suited for wind dispersal (Wilson, 1975), whilst *Enchylaena* seeds are fleshy and therefore attractive to birds, and could be dispersed via bird droppings (O'Dowd & Gill, 1986; Willson & Traveset, 2000) as planted old fields provide ready-made bird perches (trees, shrubs) that attract birds (Ferguson & Drake, 1999).

Whilst woody species richness and cover on planted old fields neared reference conditions, our first hypothesis was not supported for herbaceous species richness and to some extent cover, which was more similar to the fallow cropland than to the reference woodland. Re-establishment of herbaceous species after disturbance (e.g. fire,

mowing) can occur within a short time frame (<2 years) in more intact woodlands (Prober et al., 2007; Prober et al., 2013). We propose their establishment on planted old field plots requires further intervention to overcome abiotic and biotic thresholds (Figure 1, transition to State 4). As for woody species, barriers to the establishment of herbaceous species can include seed and seedling predation and limited seed dispersal (Standish et al., 2007; Woodall, 2010). Whilst we did not find a relationship between distance to nearest remnant and herbaceous species richness or cover, distances of 50–1550 m from remnant vegetation may limit dispersal of seeds (Table S1), even for wind-dispersed species (e.g. *Ptilotus* spp. [Hammer et al., 2018]). In addition, germination and establishment of herbaceous species may benefit from associations with mycorrhizal fungi (e.g. C4 grasses [Neuenkamp et al., 2018]) and other soil microbial communities (Eldridge et al., 2021) that may be depleted and altered in old fields.

Increased soil nutrient concentrations due to fertilizer residue, in particular P, could also pose barriers for many P-sensitive native herbs (Dwyer et al., 2015; Prober & Wiehl, 2012). Some exceptions may include native species (e.g. *Ptilotus* spp.) that can grow in very low- or high-P environments and do not show signs of P toxicity at high P levels (Hammer et al., 2020; Ryan et al., 2009). *Ptilotus polystachyus*, a species that tends to hyperaccumulate P in high-P soils, established in our old field plots; however, other *Ptilotus* species that hyperaccumulate P when available (Hammer et al., 2020; Ryan et al., 2009) did not readily recolonize the planted old fields, despite being present in nearby remnants (Tables S1 and S2). Therefore, other mechanisms, such as harsher soil biophysical properties (e.g. compaction, water infiltration), limited seed dispersal or competition with exotic species could have prevented establishment of those species.

Lack of herbaceous plant establishment has been observed in other studies across the globe (Cava et al., 2018; Munro et al., 2009; Nichols et al., 2010; Wilkins et al., 2003). Whilst most studies report successful establishment of the woody vegetation either through natural regeneration or planting, the ground layer of native grasses and herbs often remains depleted and requires further intervention (e.g. Barker et al., 2019; Pilon et al., 2018).

The increase in woody species richness and abundance coupled with the increased leaf litter and woody debris on planted old fields supports our second hypothesis, that planting can assist restoration towards the woodland reference. As predicted though, logs were an exception due to extensive time-lags in log formation (Vesk, Nolan, et al., 2008). Whilst critical for structural ground layer complexity and resource provision (Barton et al., 2011), logs take well over a century to develop (Vesk, Nolan, et al., 2008) and young planted old field sites may therefore require further intervention such as the addition of fine and coarse woody debris to accelerate progression towards a reference state (Figure 1, State 5).

Consistent with our third hypothesis, exotic species cover remained higher on the planted old field plots than the woodland reference plot, and planted trees and shrubs in the inter-rows did not facilitate a reduction in exotic species cover (Table S3). Many exotic species have highly competitive traits (abundant seeds, rapid germination and growth), and can therefore outcompete native species in high



nutrient environments (e.g. Dorrrough et al., 2011; Dwyer et al., 2015; Lai et al., 2015). However, exotic species cover may reduce over time when native trees and shrubs outcompete exotic species by reducing access to light and water (e.g. Middleton et al., 2010). Indeed, it will be important to track recovery beyond 10 years.

#### 4.1 | Implications for restoration practices and future research

To achieve establishment and persistence of the herbaceous vegetation layer in woodlands, thresholds to recovery need to be explored. Elevated soil nutrients, soil biophysical conditions, competitive exotic species, limited seed availability and seed predation might all pose barriers to restoration. However, these could vary considerably among species and depend on agricultural land-use history and time. Future research will need to disentangle hypothesized and actual barriers, and species-specific thresholds. A trait-based approach may be suitable for determining similarity among species responses and interventions that would work for groups of species (Figure 1, State 4). Chemical or other control of exotic seed predators and early-germinating exotic weeds and subsequent seeding or planting of native grasses and forbs may assist establishment by reducing competition for resources and overcoming seed limitation. However, if this is not successful, more experimentation is needed to test interventions to overcome multiple thresholds posed by P enrichment, seed limitations, exotic invasions, soil biophysical limitations, soil microbial communities and their interactions.

## 5 | CONCLUSION

A combination of planting and volunteer recruitment of trees and shrubs was effective for achieving an increase in native plant species richness and cover in planted old fields. However, the lack of establishment of native herbaceous species in the planted old fields requires further investigation to improve biodiversity outcomes. Indeed, future research focused on overcoming barriers to recovery of herbaceous species offers significant potential to achieve recovery close to vegetation reference conditions (Figure 1, Box 4).

### ACKNOWLEDGEMENTS

This study was funded by an Australian Postgraduate Award, a scholarship awarded to T.P. by Bush Heritage Australia as part of T.P.'s doctoral dissertation, project funds provided by Carbon Neutral Pty Ltd and support from the Smart Farms Program of the Australian Government's National Landcare Program. We particularly thank Ann Gunness for expert assistance with plant identification and all landholders who generously provided information and access to their land. Thanks to Sue McIntyre for providing useful comments on a draft version. The authors wish to acknowledge and pay respect to the Traditional Owners of the land on which this study was conducted: the Yamatji and Yued people.

### CONFLICT OF INTEREST

The authors declare no conflict of interest.

### AUTHORS' CONTRIBUTIONS

TP, SMP and RJS conceived the ideas and designed methodology. TP collected the data. TP analysed the data with assistance from SMP and RJS. TP led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

### DATA AVAILABILITY STATEMENT

Data are available from the Terrestrial Ecosystem Research Network (TERN) data discovery portal, <https://doi.org/10.25901/c050-ca34> (Parkhurst, 2021).

### PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1002/2688-8319.12097>.

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## SUPPORTING INFORMATION

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

**How to cite this article:** Parkhurst, T., Prober, S. M., & Standish, R. J. (2021). Recovery of woody but not herbaceous native flora 10 years post old-field restoration. *Ecological Solutions and Evidence*, 2:e12097. <https://doi.org/10.1002/2688-8319.12097>