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Patterns and drivers of natural regeneration on old-fields in semi-arid floodplain ecosystems

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Abstract

Socio-economic and environmental drivers are causing large scale abandonment of agricultural land worldwide. Simultaneously, there is growing recognition that urgent and widespread revegetation is required in our agricultural landscapes to restore biodiversity, ecosystem services and promote carbon sequestration. The design of effective revegetation strategies, however, can be limited by a lack of knowledge regarding patterns and processes of regeneration. Here, we examine naturally regenerating woody vegetation on 12 old-fields and compare this to paired remnant vegetation across four regions of a semi-arid agricultural area in eastern Australia. We found that naturally regenerating vegetation on old-fields exhibited similarities to remnant vegetation in terms of composition but varied substantially with respect to key structural attributes. Woody vegetation tends to regenerate in these old-fields with relatively high density given sufficient time (~ 30-40 years), but prior to this, very limited structural recovery occurs at all. The composition and richness of tree seedling and shrub assemblages did not differ between remnant and old-field areas. However, tree assemblages in remnant areas differed in composition and had higher species richness. Old-fields had extremely low numbers of exotic trees and shrubs. Simultaneously, most dominant native species present in the remnant vegetation were also observed in regenerating old-fields, contributing to a low degree of compositional difference between old-fields and remnant areas overall. The abundance of paddock trees, time since abandonment and mean annual rainfall are key drivers influencing natural regeneration of these old-fields. We recommend that natural regeneration is a viable form of restoration of old-fields in the northern Murray-Darling Basin given sufficient time.

Keywords: agriculture, agroecological systems, passive regeneration, restoration, spontaneous succession.

1. Introduction

Socio-economic and environmental drivers have resulted in considerable agricultural land abandonment worldwide (Cramer et al., 2007: Benayas et al., 2017). The global extent of old-fields (formerly cultivated land that has been abandoned) has rapidly increased since the 1950s, with over 200 million ha estimated to be present in 1990 (Ramankutty & Foley, 1999) – a trend which can be expected to continue in response to climate change and associated shifts in land-use (Hobbs & Cramer, 2007). At the same time, there is increasing acknowledgement that substantial and urgent revegetation is required in the world's agricultural landscapes to halt current trajectories of biodiversity loss, restore critical ecosystem services and remediate the effects of climate change (Tilman et al., 2001; Asbjornsen et al., 2014). Therefore, it is vital that we investigate and understand the most effective methods for restoring vegetation in abandoned farming areas (Bowen et al., 2007).

Active restoration of vegetation, involving the addition of seeds or planting of juvenile plants, is a popular ecological restoration method across many different habitats (Lindenmayer et al., 2010; González et al. 2015). Such interventions, however, typically entail high costs and intensive maintenance, such as the need to care for sown or planted trees (Marliana & Ruhe, 2014; Cesar et al., 2018). This renders such interventions applicable only to relatively small areas. Active restoration also has a high risk of failure due to a range of potential abiotic constraints hindering the regenerative process (Clark et al., 2007), including unsuitable microclimates for seedlings establishment (Silvestrini et al., 2012) and competition for light and resources from grass and groundcover (Peterson et al., 2014). As a result, active restoration projects can often be costly and unsuccessful, leading to unsatisfactory biodiversity outcomes (Crouzeilles et al., 2017).

Natural regeneration, whereby vegetation is allowed to regrow via in situ or dispersed seeds, with minimal human intervention, represents a major alternative to active forms of restoration for both old-fields and other altered habitats (Prach & Hobbs, 2008; Prach et al., 2013; Prach et al., 2016). This approach to revegetation entails relatively low costs and can be applied over much larger spatial areas; therefore, it has a huge potential to contribute to the restoration of old-fields (Albert et al., 2013). Recent studies suggest that natural regeneration can be effective in delivering a range of ecosystem services and biodiversity outcomes (Sojneková & Chytrý, 2015), providing a low-cost means of carbon sequestration (Evans et al., 2015), building connectivity in fragmented agricultural landscapes (Sanchez-Cuervo et al., 2012) and providing valuable habitat for wildlife and understorey plants (Good et al., 2012).

For effective natural regeneration to occur, there must be a sufficient supply of viable plant propagules present or arriving at a site (Kimmel et al., 2010). Plant propagules can be transported throughout the landscape via wind, water or animals, or stored within soil seed banks or other propagule banks, including aerial seed banks where these persist (Middleton et al., 2003; Williams et al., 2008). Remnant trees (locally referred to as ‘paddock trees’ within modified landscapes) can also provide an important supply of seed and may be particularly valuable for restoring old-fields (Manning et al., 2006; Pangou et al., 2009) by influencing abiotic conditions which may, in turn, affect the capacity of plant propagules to successfully germinate and establish (Good et al., 2014). Shading, for example, as provided by large remnant trees, has a strong influence on the germination and establishment of tree and shrub species (Neilan et al., 2006). Rainfall and, in riparian and floodplain habitats, flooding are also vital for the successful establishment of plants across a range of environments from arid lands (Capon & Brock, 2006) to tropical forests (dos Santos et al., 2017). Flooding plays a further key role in the dispersal of seeds throughout riverine landscapes as well as influencing plant establishment and reproduction, thereby greatly influencing the structure of vegetation communities in floodplain and riparian ecosystems (Capon, 2015; Capon et al., 2016; Murray et al., 2019). Soil condition is also likely to influence successful vegetation establishment in old-fields where nutrients may have been depleted or chemicals added during prior agricultural use (Standish et al., 2006; Do Vale et al., 2015).

Overall, the capacity for old-fields to successfully revegetate passively can be expected to be strongly influenced by the history of cultivation, previous land-use type and the time since abandonment (Benjamin et al., 2005; Holz et al., 2009). The history of cultivation and previous land use will play a key role in determining the patterns and success of natural regeneration due to the degree of local and landscape-scale antecedent ecological modification and degradation (Dawson et al., 2020). The establishment and long-term survival of vegetation on old-fields will be further affected by management practices, such as grazing control, following initial regeneration (Ne'eman, 2011). Time since abandonment is particularly important in determining the opportunity for successful recruitment of vegetation in the context of the site-specific abiotic and biotic conditions (Aide et al., 2000; Stroh et al., 2012). Additionally, trajectories of vegetation regeneration may reflect threshold dynamics which are important in predicting species recovery (Groffman et al., 2006; Bourgeois et al., 2016). Species in harsh or unpredictable environments, such as semi-arid floodplains, may not recover in a gradual and predictable successional trajectory. Rather, they are more likely to exhibit abrupt increases in vegetation cover, with regeneration often accelerating in response to favourable environmental events (Bestelmayer, 2006; Suding & Hobbs, 2009).

Understanding different pathways and drivers of natural regeneration is critical for informing the development of effective strategies for the revegetation of large areas of abandoned agricultural land (Dorrough and Moxham, 2005). Such knowledge can guide the prioritisation of active versus passive revegetation approaches and suggest under which circumstances each approach might be favourable. Here, we explore natural regeneration patterns on old-fields across agroecological floodplain landscapes of the northern Murray-Darling Basin in semi-arid eastern Australia. We examined vegetation composition and structure in 12 old-field sites and compared this to paired sites with remnant vegetation across four regions of the northern Basin, distributed along a broad east-west aridity gradient. We sought to understand vegetation regeneration patterns and pathways occurring in the study area and determine some of the key drivers, including the effects of time since abandonment. More specifically, we sought to address these research questions:

1. How do major structural habitat characteristics differ between regenerating old-fields and adjacent remnant patches of vegetation on semi-arid floodplains?
2. How does woody vegetation composition and structure vary between naturally regenerating old-fields and adjacent remnant patches of vegetation on semi-arid floodplains?
3. What are the key environmental factors driving variation in woody vegetation composition on semi-arid floodplain old-fields?

2. Methods

2.1 Study area

This study was conducted in the northern Murray-Darling Basin, a semi-arid agricultural area in eastern Australia (Figure 1) with low average rainfall (< 600 mm annually) and nutrient-poor soils. The area is dominated by large dryland river systems with extensive floodplains that are characterised by extremely variable flow regimes (Walker et al., 1995; Bunn et al., 2006). Study sites were selected across four major regions, labelled by their closest towns (Bourke, Moree, Mungindi and St George), within the northern Murray-Darling Basin to represent a broad east-west aridity gradient, with higher rainfall and streamflow in the east and drier conditions in the west (Figure 1, Table 1).

Overstorey vegetation on floodplains of the area is dominated by *Eucalyptus coolabah* Blakely & Jacobs (coolibah) woodlands, while riparian areas are typically occupied by a mix of *E. camaldulensis* Dehnh (river red gum) and *E. coolabah.* Mid-storey shrub layers, where they occur, mainly comprise *Duma florulenta* (Meisn) (tangled lignum). In these regions, understorey vegetation is highly dynamic (Capon, 2005), often comprising chenopod subshrubs (e.g. *Sclerolaena muricate* (Moq.) Domin *var. muricata*), perennial grasses and hardy forbs (e.g. *Portulaca* sp., *Medicago polymorpha L.* and *Sporobolus* sp.) during dry periods (Good et al., 2012), and a diverse range of aquatic, amphibious and terrestrial forbs, grasses and sedges during wetter periods.

Land-use in the region is dominated by irrigated and dryland cropping, as well as cattle and sheep grazing. Europeans first settled in the northern Murray-Darling Basin in the mid-1800s, where they grazed extensive flocks of sheep, using riverboats along the Darling River to export the wool. Extensive cropping did not begin in the northern Murray-Darling Basin until the 1950s (Walker & Thoms, 1993). Since then, multiple extended periods of drought and climate change have led to the abandonment of many cropped fields. Land-use change, including conversion of cropped fields to grazing or conservation land, has also been triggered by various environmental policies (Evans et al., 2015), as well as in response to the effects of greater environmental flow delivery in these catchments, i.e. increased inundation of floodplain crops (Docker & Robinson, 2014).

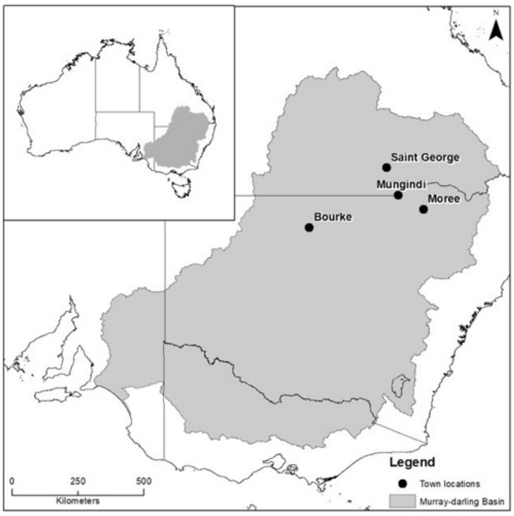

Figure 1: Map illustrating the position of the four study locations in the Murray-Darling Basin. Inset show's location in Australia.

Region	**Mean annual* rainfall (mm)**	**Average: Max/ min summer & winter temps* (°C)**	**Major catchment**	**Ages of old-fields in each region.**	**Previous cropping**
Moree	567.5	Summer – 34.3/ 20.5 Winter – 18.4/4.5	Gwydir	33 7 20	Unknown cropping, Irrigated cotton, Irrigated cotton.
Mungindi	487.8	Summer – 36.1/ 20.8 Winter 19.9/4.7	Barwon-Darling	5, 10 20	Irrigated cotton, Irrigated cotton Unknown cropping
St George	459.1	Summer – 35.8 – 22.4 Winter – 19.7/ 5.2	Condamine-Balonne	8 28 33	Unknown cropping, Unknown cropping, Unknown cropping
Bourke	295.3	Summer – 37.7/22.8 Winter- 18.6 – 4.2	Barwon-darling	9 9 40	Irrigated cotton, Irrigated cotton Dryland wheat

Table 1: Key characteristics of study sites in each region. Moree mean annual rainfall and temperatures are from 1995-2020. Mungindi from mean average rainfall and temperatures is from 1991-2020, St George mean rainfall and temperature are from years 1997-2020 and Bourke's mean average rainfall and temperature are from years 1998 – 2020. Average max/min summer & winter temperature are the average maximum and minimum temperature during the recorded period for summer in January and for winter in July.

*Source: Bureau of Meteorology, 2020.

2.2 Vegetation survey

Study sites were selected in each region to represent two broad land-use histories: remnant vegetation and old-fields (Supplementary material 2). Remnant vegetation was defined as that existing in areas that had never been cultivated for cropping, although these areas have all been, or continue to be, used for livestock grazing and were included in the study design as reference ecosystems. Old-fields comprised areas that had been historically cropped but abandoned for at least five years (Table 1), with or without current livestock grazing. Old-fields ranged in size from relatively small patches (~0.02 km^2) straddling riverbanks, to large fields (the biggest at ~0.52 km^2) representing entire abandoned cropping paddocks. Information regarding land-use history was gathered from landholders via semi-structured interviews and tours of the properties. Time since abandonment was determined through the interviews and information provided by landholders.

All sites were located within floodplain areas and varied in distance from the closest river channel from 33 to 1 670 meters. Floodplains were identified based on the set of wetlands species (i.e. *E. coolabah and Duma florulenta*) present at the site and/or black cracking clay soil in addition to landholder advice. Floodplains of the northern Murray-Darling Basin are extremely flat with complex patterns of wetting and drying that do not necessarily reflect proximity to channels. Consequently, selected sites are likely to have represented a range of flood histories. We used a paired site design by identifying remnant patches within close proximity to each old-field to minimise differences between pairs in soil characteristics, flood history, climatic conditions, dominant vegetation types and land management practices. Paired sites were, on average, 706 meters apart (± 694 meters). A paired old-field and remnant site are referred to here as a 'location'. In total, we surveyed 12 different locations with three in each region. Vegetation surveys were conducted between July 2018 to March 2019. At the time of sampling between late 2018 and early 2019, the entire northern Murray-Darling Basin had experiened a severe drought since 2017, with the lowest rainfall in over 100 years (Bureau of Meteorology, 2019).

At each site, vegetation surveys of all woody strata (i.e. trees, tree seedlings and shrubs) were conducted within three randomly positioned replicate 50 m x 50 m plots, each of which was separated by at least 150 meters. In each plot, we counted and identified every tree and recorded its height and diameter at breast height (DBH). Additionally, all shrubs and tree seedlings in each plot were identified, counted and their height was recorded. Woody plants were considered trees when over 1 m tall and seedlings were under 1 m in height, while shrubs were those woody plants with multiple stems of small DBH (<5 cm) and up to 2 m tall. There were no species found within the surveys that were non-woody and over 1 meter tall. All plant species were named according to the Flora of New South Wales online database (https://plantnet.rbgsyd.nsw.gov.au).

Understorey vegetation and environmental characteristics were surveyed in ten 1 m^2 quadrats randomly positioned within each plot. Understorey vegetation included all vegetation, dead or alive, below 1 m in height. Within each of these 1 m^2 quadrats, % ground cover, leaf litter and bare ground was recorded. Canopy cover was recorded using a spherical densiometer at the four compass directions (N, S, E, W) of each quadrat. The length of all coarse woody debris (CWD) with a diameter of at least 6 cm was also recorded at the plot-scale. Finally, five soil samples of 5 cm diameter x 10 cm depth were collected randomly from each plot, aggregated and transported back to Griffith University. Soil samples were used to assess soil salinity and acidity at each site (Hardie & Doyle, 2012). These were measured in the laboratory by adding 10 g of soil into 50 ml of distilled water, stirring for 30 minutes, and then inserting a pH/ECM250 Meterlab probe (Copenhagen) into the water to get a pH and electric conductivity (EC) reading.

Several additional environmental variables expected to play a role in shaping natural regeneration were also calculated from available data. The number of paddock trees was calculated by summing the total number of trees present in a plot with a DBH over 30 cm. Distance from remnant patch was calculated for each old-field by measuring the distance from the middle of each plot (where a GPS location point was recorded during fieldwork) to the closest point where there was a patch of vegetation (two or more trees), as determined from inspection of imagery in Google Earth Pro. Coarse woody debris was measured as the total length of woody debris over 6 cm in diameter in each plot. There is no reliable flooding data available for the sites surveyed.

2.3 Data analysis

A mixed-effects model was used to investigate differences in key habitat characteristics in relation to land-use history (remnant and old-field), which was a fixed factor. Region and location were included in the model as random effects with location nested in region. Prior to analysis, data were log (base-e logarithm) or square root transformed where necessary to meet the assumptions of the model. Variation in the abundance and species richness of each woody vegetation strata was explored using a generalised linear mixed model with a Poisson distribution to detect significant differences in abundance and species richness between land-use histories. Abundances were calculated by summing the total number of individuals in each stratum within each plot. Species richness values represented the total number of different species within each stratum within each plot. For the tree abundance analysis, one pair of sites from St George was excluded as an outlier because of the extremely high abundances of *Eucalyptus coolabah* seedlings.

Relative abundance and species richness were also calculated for each woody vegetation strata (i.e. trees, seedlings and shrub). To create a standardised value for vegetation regeneration at each old-field plot compared to its remnant reference plot, we used the formula: $\frac{Paired\ remnant\ plot\ richness\ or\ abundance\ - Paired\ Old-field\ plot\ richness\ or\ abundance}{Paired\ Remnant\ plot\ richness\ or\ abundance} = Pair\ relative\ richness\ or\ abundance$. This formula created a relative value for metrics for stratum type abundance and vegetation type species richness.

Effects of time since abandonment on the relative abundance and richness of each stratum was then examined using a linear mixed-effects model. Two extreme outlier plots were removed from this analysis, both of which were from the old-field site in Bourke. These two plots had a lower topographic elevation than their remnant reference plots that likely caused a thicket of wetland shrubs (*Duma florulenta*) to regrow in the old-fields compared to the paired remnant and produced an extremely high relative value for shrubs.

Variation in the composition of tree, seedling and shrub assemblages between region and land-use history was examined in separate non-metric multidimensional scaling ordinations based on a Euclidean distance matrix. Euclidean distance was used as the measure of similarity between data points due to the number of 0 values in the dataset. Before analysis, the data was Hellinger transformed to meet the assumptions of homogeneity (Legendre & Gallagher, 2001). Analysis of similarities (ANOSIM) was used to test for significant differences in composition between regions and land-use history. Multivariate analyses were conducted with the 'vegan' package (Oksanen et al., 2019) within the R program (version 1.2.5001, R Development Core Team, 2019).

To relate the composition of old-field vegetation assemblages to habitat conditions, a distance-based redundancy analysis (RDA) using Hellinger transformed species abundance data was performed for each stratum (i.e. trees, seedlings shrubs) in the vegan package within R (Oksanen et al., 2019). Prior to this analysis, explanatory factors were standardised due to their different physical units. As a constrained ordination, RDA examines the relationship between a response variable matrix and explanatory variable matrix through regression and ordination. If a full RDA model was significant, then a stepwise model building approach was conducted. Terms that were not significant were removed from the model (significance level, at $P<0.05$). The final model with each significant term was then tested using a permutation ANOVA on 999 permutations (Borcard et al., 2018). Due to the low number of canonical axes, their significance was not tested (Legendre et al., 2011). All statistical analysis was undertaken in R version 4.0.2 (2020-06-22).

3. Results

3.1 Habitat characteristics

Land-use history had a significant influence on multiple habitat characteristics. Coarse woody debris ($P = <0.000$, Marginal $R^2 = 0.196$), % litter cover ($P = <0.000$, Marginal $R^2 = 0.072$) and canopy cover ($P = <0.000$, Marginal $R^2 = 0.469$) were all higher in remnant vegetation patches than old-fields (Figure 2). There was also significantly more bare ground in old-fields than in remnant areas ($P = 0.016$, Marginal $R^2 = 0.0326$), but no difference in ground cover between remnant and old-fields. Average soil pH was higher in old-fields than in remnant vegetation patches ($P = <0.000$, Marginal $R^2 = 0.070$), while soil EC was higher in remnants than in old-fields ($P = 0.035$, Marginal $R^2 = 0.040$).

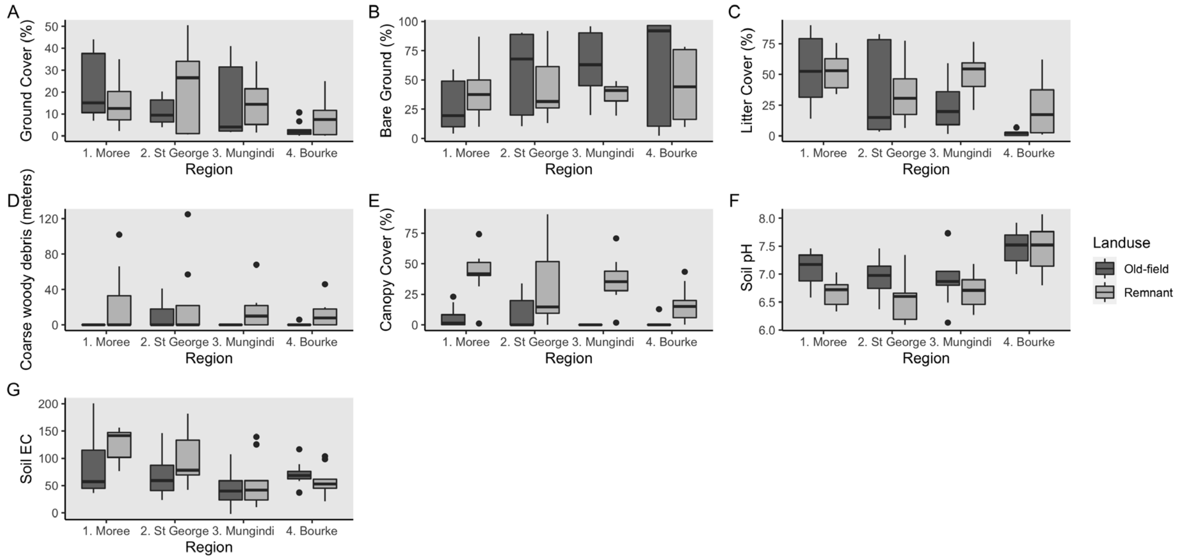

Figure 2: Boxplots displaying habitat characteristics between old-fields and remnant vegetation within different regions of the study area. A) ground cover (n = 72), B) bare ground (n = 72), C) litter cover (n = 72), D) coarse

woody debris (n = 72), E) canopy cover (n = 72), F) soil pH (n = 72) and G) soil EC (n = 70). Mean values are shown +/- standard error.

3.2 Woody vegetation floristics

In total, 4,182 trees were surveyed across all 72 plots, comprising 26 tree species occurring as mature individuals (Table 2) and an additional 772 seedlings representing 18 tree species (Table 2). Two species were only observed as seedlings, *Hakea leucoptera* and *Melaleuca trichostachya. Eucalyptus coolabah* was the most abundant tree recorded and was present in the overstory at 86 % of plots. *E. coolabah* was also recorded as both an adult and as a seedling in all regions and under both land-use histories. Likewise, *Acacia stenophylla* was recorded as an adult and seedling within all regions and land-use histories. A total of 971 shrubs were recorded from all plots representing 11 different species. *Duma florulenta* was by far the most abundant and widespread shrub across all plots, followed by *Vachellia nilotica* and *Chenopodium desertorum*. It should be noted that there was only one exotic tree species and one exotic shrub species found throughout all plots.

Table 2: Total richness of woody (tree, seedling and shrubs) species recorded in the vegetation survey in each region and land-use history. *RV= Remnant vegetation, Of = old-field,* ○ = Both seedling and trees, ● = Just trees and ▲= Just seedling, * = exotic species. All species names follow nomenclature provided by NSW Flora Online (https://plantnet.rbgsyd.nsw.gov.au)

	Bourke		Mungindi		St George		Moree	
Species	OF	RV	OF	RV	OF	RV	OF	RV
Tree & Seedlings								
Acacia cambagei R.T.Baker			○	○	●			
Acacia harpophylla F.Muell. ex Benth.				○				
Acacia pendula A.Cunn. & G.Don		▲			○		●	
Acacia salicina salicina Lindl.					○		○	○
Acacia stenophylla A.Cunn. ex Benth.	▲	○	▲	○	○	○	●	○
Atalaya hemiglauca (F.Muell.) F.Muell. ex Benth.		●	▲		●			●
Brachychiton populneus (Schott & Endl.) R.Br.				●				
Callitris columellaris F.Muell.				●				

Casuarina cristata Miq.			▲	●				
Eremophila bignoniiflora (Benth.) F.Muell.	●	●		○			○	●
Eremophila longifolia (R.Br.) F.Muell.				●				
Eremophila mitchellii Benth.				○	●			
Eremophila oppositifolia R.Br.	●	●						
Eremophilla spp. 1		●						
Eucalyptus camaldulensis Dehnh.		●			●	●		●
Eucalyptus coolabah Blakely & Jackobs	●	○		○	○	○	○	○
Eucalyptus largiflorens F.Muell.		●						
Eucalyptus populnea F.Muell.				○	○		●	
Flindersia maculosa (Lindl.) Benth.				●				
Geijera parviflora Lindl.			▲	●				
Hakea leucoptera R.Br.			▲					
*Ligustrum lucidum** Aiton			▲	○				
Melaleuca trichostachya Lindl.			▲					
Myoporum platycarpum R.Br.		●						
Myrtaceae spp. 1								●
Ventilago viminalis Hook.		▲		●				●
Shrubs								
Apophyllum anomalum F.Muell.				●				
Atriplex nummularia Lindl.				●				
Bursaria spinosa Cav.					●			
Chenopodium auricomum Lindl.	●							
Chenopodium desertorum (J.M.Black) J.M.Black subsp. microphyllum	●			●			●	●
Duma florulenta (Meisn.) T.M.Schust.	●	●		●	●	●		
Lycium ferocissimum Miers*							●	●
Maireana pyramidata (Benth.) Paul G.Wilson		●						
Neobassia proceriflora (F.Meull.) A.J.Scott				●				
Unknown shrub 1				●				
Vachellia farnesiana (L.) Wight & Arn.				●	●		●	●
Species richness for trees	**3**	**9**	**1**	**15**	**9**	**3**	**6**	**8**
Species richness for seedlings	**1**	**4**	**7**	**8**	**5**	**2**	**3**	**3**
Species richness for shrubs	**3**	**2**	**0**	**7**	**3**	**1**	**3**	**3**
Total richness	**7**	**13**	**8**	**22**	**12**	**4**	**9**	**11**

3.3 Woody vegetation structure

Tree abundance (*P* = < 0.0001, Marginal R^2 = 0.667) and species richness (*P* = < 0.0001, Marginal R^2 = 0.385) were significantly higher in remnant plots compared with old-fields in all four regions (Figure 3). More seedlings were also present in remnant plots (*P* = 0.033 Marginal R^2 = 0.068), but no difference in the species richness of seedlings between land-use histories was detected. Likewise, there was no difference in shrub abundance or richness between land-use histories.

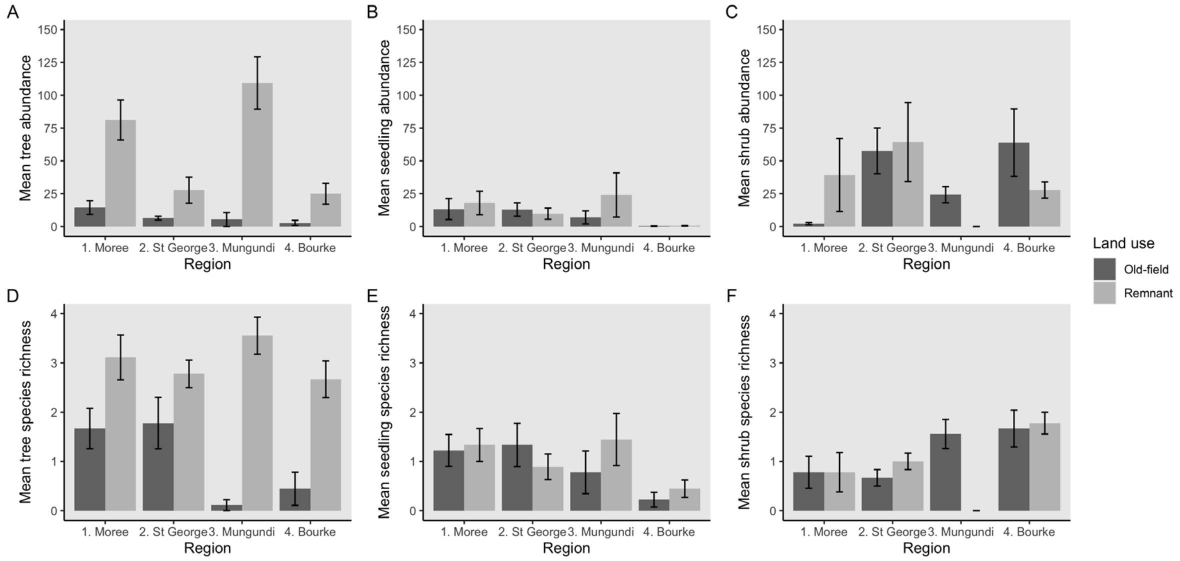

Figure 3: Mean A) trees abundance, B) seedlings abundance, C) shrubs abundance, D) tree species richness, E) tree seedling species richness and F) shrub species richness in each land history type and region. N.B. Error bars display standard error.

With greater time since abandonment, the relative abundance of trees (*P*= 0.0467, adjusted R^2 = 0.087) and shrubs (*P* = 0.0007, adjusted R^2 = 0.370) increased, indicating increasing abundances in old-fields relative to those of paired remnants. Similar patterns were also observed for relative species richness for trees (*P* = 0.000072, adjusted R^2 = 0.365) and shrubs (*P* = 0.00074 and an adjusted R^2 = 0.346, Figure 4). However, relative species richness and abundance did not significantly increase with time since abandonment for seedlings.

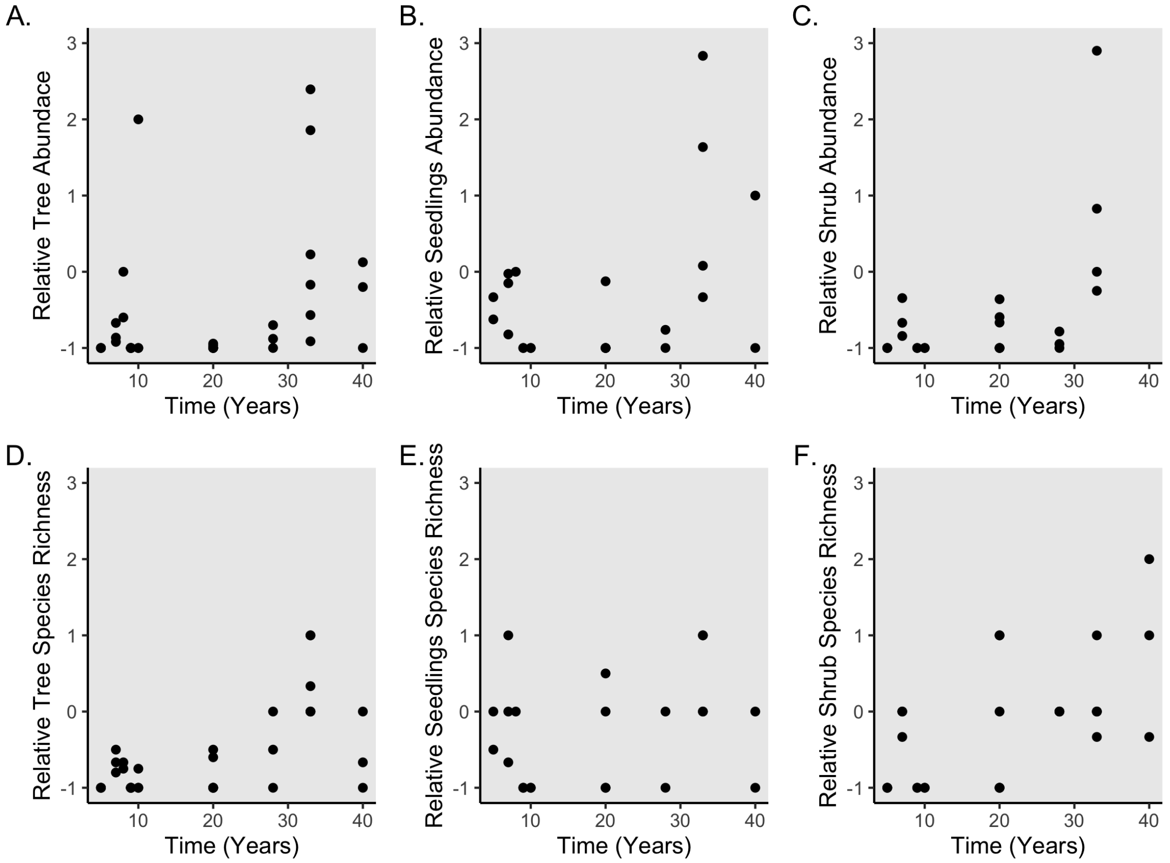

Figure 4: Relative abundance against time since abandonment (years) for trees (A), seedlings (B) and shrubs (C) and relative species richness against time since abandonment (years) for trees (D), seedlings (E) and shrubs (F). Note: relative abundance and richness values have been inverted. This has been done so that more vegetation abundance or richness in old-fields compared to paired remnant vegetation is represented in a positive value and less abundance or species richness in old-fields then remnant vegetation is represented as a negative. A 0 indicates relative abundance/richness values is equal in both land-use histories.

3.4 Woody vegetation composition

The composition of tree (R = 0.175, *P* = 0.001), seedling (R = -0.159, *P* = 0.001) and shrub (R = 0.279, *P* = 0.001) assemblages all varied significantly between regions. In contrast, composition did not differ between land-use histories for seedlings and shrubs but did for trees (R = 0.137, *P* = 0.001). This is apparent in the large amount of overlap evident in the position of plots in the shrub and seedling ordinations (Figure 5), while tree assemblages between the two land-use histories are more differentiated.

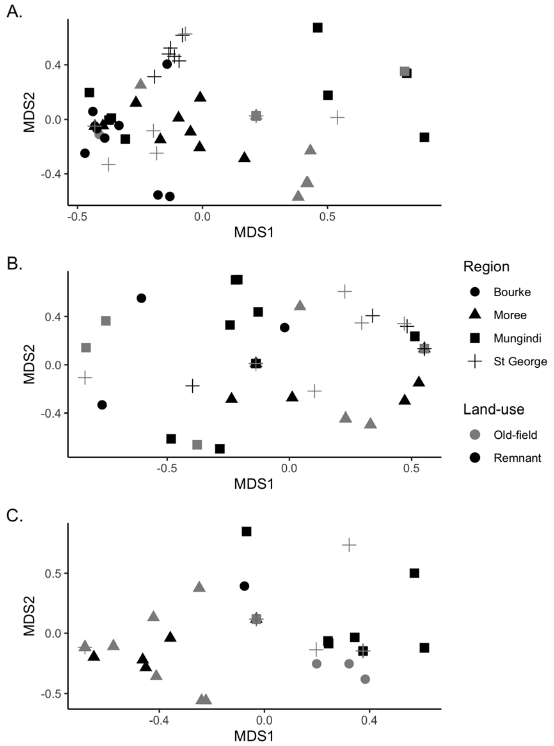

Figure 5: Non-metric multidimensional scaling ordination of A) Trees (stress = 0.11), B) seedlings (stress = 0.11), C) Shrub (stress = 0.04). Each point in the ordinations represents a plot.

RDA analysis indicated that significantly correlated habitat conditions explained 26 % of the total variation in the composition of tree assemblages (Table 3, Supplementary material 1). Significantly correlated environmental variables explained 25 % of the composition of seedling assemblages and 61 % of the composition of shrub assemblages. Variation in tree composition on old-fields was significantly associated with time since abandonment, mean annual rainfall and soil EC (Supplementary material 1, Table 3), while seedling composition could be explained by mean annual rainfall, canopy cover and number of paddock trees. Variation in shrub composition was associated with six significant explanatory variables;

time since abandonment, distance from remnant patch, canopy cover, % ground cover, % litter cover and soil EC.

Explanatory variables	**Tree**			**Seedlings**			**Shrubs**		
	Adj R^2	*F*	*P*	Adj R^2	*F*	*P*	Adj R^2	*F*	*P*
Time since abandonment	**0.063**	**3.299**	**0.018**	NS	NS	NS	**0.210**	**10.03**	**0.002**
Mean annual rainfall	**0.191**	**3.297**	**0.022**	**0.131**	**3.01**	**0.016**	NS	NS	NS
Distance from remnant patch	NS	NS	NS	NS	NS	NS	**0.530**	**3.02**	**0.028**
Canopy cover	NA	NA	NA	**0.076**	**3.806**	**0.010**	**0.49**	**3.75**	**0.002**
Number of paddock trees	NA	NA	NA	**0.065**	**2.86**	**0.008**	NS	NS	NS
% Ground cover	NS	NS	NS	NS	NS	NS	**0.308**	**5.68**	**0.002**
% Litter cover	NA	NA	NA	NS	NS	NS	**0.452**	**4.882**	**0.002**
Soil EC	**0.133**	**3.067**	**0.010**	NS	NS	NS	**0.383**	**4.90**	**0.002**
Soil Ph	NS	NS	NS	NS	NS	NS	NS	NS	NS

Table 3: Results from the RDA model analysis regarding old-field vegetation abundances with habitat condition factors. NA indicated that the factor was not included due to them not being independent to the response vectors. NS indicates that the factor was not significant.

4. Discussion

Here, we investigated the composition and structure of regenerating woody vegetation on floodplain old-fields in relation to remnant vegetation in four regions distributed along a broad aridity gradient across the northern Murray-Darling Basin, Australia. Overall, regenerating vegetation on these old-fields displayed reasonably high similarity to remnant vegetation in terms of composition, including the presence of dominant species, but exhibited substantial structural differences. Woody vegetation tended to regenerate in high densities after ~ 30-40 years, although before this time, minimal structural recovery was apparent. Key drivers influencing naturally regenerating vegetation in these old-fields were paddock trees, time since abandonment and mean annual rainfall. Given these observed responses on old-fields across the study area, we recommend natural regeneration as a viable form of revegetation in agricultural regions of the northern Murray-Darling Basin.

4.1 Habitat variation

Soil electro conductivity (EC) and pH varied between land-use histories, probably reflecting historic disturbances associated with cultivation (Standish et al., 2006). Old-fields had soils with higher pH compared to remnant sites, although all soils tested were within the neutral range. Soil pH is commonly altered by fertiliser application during cropping and differences observed here likely reflect past land management practices (Conyers et al., 2011). Soils from old-fields also had significantly lower salinity than remnant areas, as indicated by EC. Old-fields probably received more overall water through irrigation than remnant areas historically. Consequently, more soluble salts may have leached deeper into the soil profile (Rengasmy, 2002). This study only tested the top 10 cm, however, with previous research in arid irrigated areas revealing higher salinities deeper in the soil profile (i.e. >10 cm) (Feng et al., 2005).

Other habitat characteristics also differed predictably between old-fields and paired remnant vegetation, especially those associated with woody canopy vegetation. Canopy cover, coarse woody debris and leaf litter were all significantly higher in remnant patches. These characteristics are important determinants of vegetation function, particularly habitat provision to terrestrial fauna (Mac Nally et al., 2001), and can also affect vegetation dynamics by influencing germination and seedling establishment (Peterson et al., 2014). Capon et al. (2017) demonstrated a strong influence of shade and litter on understorey plant communities establishing from soil seed banks in response to flooding from riparian habitats across the northern Murray-Darling Basin. Despite this contrast in structural habitat, however, there was no significant difference in the amount of groundcover vegetation between old-fields and remnant plots in the present study. The region was experiencing a drought at the time of sampling, accounting for the very sparse groundcover observed. During drought, recent antecedent conditions such as local rainfall and grazing pressure, may be more likely to drive groundcover than land-use history (Capon & Reid et al., 2016). Variation in groundcover between old-fields and remnants may therefore only be apparent following more favourable wet conditions, reflecting potential differences in soil seed banks and/or environmental filters such as shading (Capon et al., 2017)

4.2 Composition of regenerating old-field vegetation

The composition of woody seedling and shrub assemblages observed here was similar between old-fields and remnant vegetation, although remnants tended to have more tree species with different assemblages compared with adjacent old-fields. Overall, however, the species pool was similar between the two land-use histories with most trees, shrub and seedling species found within both old-fields and remnant areas in at least one study location throughout the four study regions (Table 2). The high similarity in assemblages is explained mainly by the presence of key dominant species (i.e. *Eucalyptus coolabah, Acacia stenophylla*, *Duma florulenta*) across most old-fields and remnant areas within all regions (Table 2). Twelve of the 37 woody species were only found in remnant areas, although nine were observed solely in a single location in Mungindi. The species richness of trees and seedlings was greatest in this one location of Mungindi due to its marginal floodplain location, with terrestrial species (e.g. *Brachychiton populneus, Eucalyptus populnea*, *Eremophila mitchellii*) present here in addition to common floodplain species. The other three species that were only found in remnant plots were all observed in Bourke, on the far end of the aridity gradient. The distinct tree assemblages and greater tree species richness in remnant areas compared to old-fields highlights the high biodiversity value that remnant areas hold within agricultural landscapes (Howorth & Pendry, 2006). Disturbance from agricultural land-use can alter biotic and abiotic factors which can take a long time to recover, particularly in harsh and dry environments (Creamer et al., 2008). Nevertheless, the relatively small differences observed between old-fields and remnant patches in woody vegetation composition demonstrate a promising capacity for natural regeneration to occur in old-fields in this study area (Staples et al., 2019).

Interestingly, despite the history of agriculture at these sites, very low numbers of exotic woody species were recorded, with only one exotic tree observed in Mungindi and one exotic shrub in Moree. Old-fields are often considered hotspots for exotic species invasions due to high levels of recent disturbance (Csecserits et al., 2011). Schmitt et al. (2019) found that old-fields in semi-arid agricultural landscapes of Kenya were invaded by mono-dominant thickets of *Lantana carmara* which grew after land-owners fallowed their paddocks, in turn suppressing the regeneration of native flora through resource competition. Similarly, Martin et al. (2004) found that the exotic invasion of a non-native tree species delayed the recovery of native plant diversity on tropical old-fields in the Dominican Republic due to the ability of non-native species to colonise disturbed areas and outcompete natives, resulting in different species assemblages and stunted regeneration. Comparable woody exotic invasion was not observed in the current study, possibly reflecting low levels of exotic species' propagule supply and/or an inability for exotics to successfully establish due to these dryland floodplains' harsh conditions (Moore & Elmenford, 2006; Warren et al., 2013).

4.3 Structure of regenerating old-field vegetation

While the composition of woody vegetation assemblages was similar between old-fields and remnants, vegetation structure exhibited substantial differences in relation to land-use history.

In younger old-fields, very little woody vegetation structure was observed. However, in the more mature old-fields (~ 30 – 40 years), tree density was considerably higher than in adjacent remnants. Woody vegetation of semi-arid floodplains typically reflects flooding patterns (Capon & Brock, 2006). Stand dynamics of *E. camaldulensis*, *E. largiflorens* and *E. coolabah*, all dominant overstory species in this study, are strongly driven by flooding, with dense recruitment typically occurring in relation to flooding events (Maher, 1995; Moxham et al., 2018). Remnant vegetation and areas abandoned for longer are therefore more likely to have experienced more flooding events (or sequences of events) promoting recruitment (Maheshwari et al., 1995). Indeed, very little recruitment appears to occur in these old-fields without flooding, reflecting the boom and bust natural of semi-arid floodplain ecosystems (Bunn et al., 2006).

Our study also suggests that after 30 years, woody plants had begun to grow in higher abundances on old-fields than paired remnant plots – a phenomenon often referred to as ‘woody thickening’ (Hoffman & Connor, 2008). Dense regenerating *Eucalyptus coolabah* woodlands on cleared land elsewhere in the Murray-Darling Basin, for example, are structurally, but not floristically, different to remnant patches (Good et al., 2012). This thickening pattern of regrowth in agricultural regions has been observed throughout Australia with cleared or disturbed areas often naturally regenerating with an increased abundance compared with reference conditions (Costello et al., 2000; Dwyer et al., 2010; Good et al., 2011). The increase in both woody stem density and individual abundance is often assumed to reflect changes in local or regional landscape disturbance regimes (McGregor et al., 2016), including flooding (Bren, 1992), rainfall patterns (Fensham et al., 2005) and fire (Roques et al., 2001). Woody thickening globally is also frequently attributed to broader climate changes since the industrial revolution, particularly rising CO_2 concentrations (Prentice et al., 2011).

4.4 Factors driving natural regeneration on old-fields

Naturally regenerating vegetation on old-fields often exhibits strong heterogeneity in relation to regional differences (Ruskule et al., 2016). Here, the composition and abundance of trees exhibited strong regional patterns across the northern Murray-Darling Basin. More trees occurred in sites in the wetter eastern regions and distinct assemblages were apparent between the four regions. Composition of tree assemblages in the northern Murray-Darling Basin is very likely to be at least partially driven by mean annual rainfall and therefore flooding. Time since abandonment and soil EC also significantly influenced the composition of tree assemblages on old-fields, suggesting an influence of previous land-use practices and anthropogenic disturbances (do Nascimento Oliveira et al., 2019; dos Santos et al., 2019). Greater time since abandonment allows vegetation more opportunities to recolonise and for possible successional processes to occur (Holl et al., 2018; Vacek et al., 2019). Regeneration is often influenced by soil characteristics including salinity, particularly in agricultural landscapes where a mosaic of land-use histories tends to occur (Mora et al., 2012). Salinity can increase due to cropping, irrigation and land management, particularly in semi-arid regions, often limiting vegetation growth (Corwin et al., 2003).

The species richness, abundance and composition of woody seedling assemblages on old-fields also exhibited regional differences in relation to the aridity gradient, reflected here by mean annual rainfall. Studies in agricultural areas of the southern Murray-Darling Basin have failed to detect a similar effect of mean annual precipitation on the regeneration of Eucalyptus species with observed regeneration often not differing between subregions (Sato et al., 2016: Sato et al., 2019). This may be due to the more temperate climate and higher mean average rainfall in the southern part of the Basin where recruitment may not be so limited by water availability. In these studies, species richness and assemblage composition of tree seedlings was not affected by time since abandonment, suggesting that where strong regional gradients are absent, seedlings may be more influenced by local antecedent conditions (Matinez-Ramos et al., 2018). Canopy cover and the abundance of paddock trees were identified in our study as significant determinants of seedling composition on these old-fields. Existing canopy probably contributes to regenerating vegetation through both seed supply (Jensen et al., 2008) and facilitation effects, including shading from harsh conditions (Manning et al., 2006).

Shrub species richness and composition on old-fields also exhibited significant regional differences. A clear aridity gradient was also apparent with higher species richness in more arid regions. Shrub assemblages on old-fields were driven by time since abandonment, with more extended periods of regeneration associated with higher abundance, species richness and distinct species composition. Shrub assemblages were also driven by apparent facilitation effects from canopy cover and distance from remnant patch, which may provide seed supply and shading effects (Cesar et al., 2019; Ramirez-Pinero et al., 2019). Shrubs on old-fields may be acting as nurse plants, as higher ground cover and litter cover were associated with shrub assemblages (Tölgyesi et al., 2018). These results are consistent with those of Capon et al. (2015) who found that *Duma floruenta* was associated with higher levels of ground cover and litter, demonstrating the importance of shrubs for the physical and structural habitat they create and assisting in the colonisation of old-fields (Bueno et al., 2015).

4.5 Implications for restoration of floodplain old-fields in the northern Murray-Darling Basin

In semi-arid areas, such as the northern Murray-Darling Basin, which are characterised by high temperatures, low rainfall and nutrient poor-soil, abiotic stress is high and the cultivation legacy on old-fields is likely to be greater than that under more moderate climatic and edaphic conditions (Creamer et al., 2008). Nevertheless, we found that floodplain old-fields in this region have a strong capacity to naturally regenerate with woody vegetation communities of similar floristic composition to that of remnant reference sites but with an altered structure that is likely to persist for at least several decades of regrowth. Perception studies have documented people’s negative views of natural regeneration within Australia's agricultural landscapes where it is often referred to as “woody weed invasion” (Sharp et al. 2012, Stelling et al., 2017). These opinions may be hindering the conservation of naturally regenerating vegetation and acceptance of this passive approach as an appropriate restoration strategy in some regions. Results such as those presented here will be important in demonstrating to the community the potential efficacy of natural regeneration and how it might be best managed.

We identified the abundance of paddock trees as particularly important for the regenerative capacity of old-fields in this study area. Moving forward, the protection and planting of more paddock trees may, therefore, be important for providing system stability and regeneration options for the future (Manning et al., 2006; Fischer et al., 2010). Finally, large-scale factors such as altered flooding and fire regimes and climate change may have overriding impacts on the observed patterns of vegetation and need further research. In conclusion, natural regeneration appears to be a feasible approach to revegetating old-fields in this region but may require disturbance events, especially floods and longer periods of time for thinning processes to occur to promote structural attributes more aligned with remnant vegetation.

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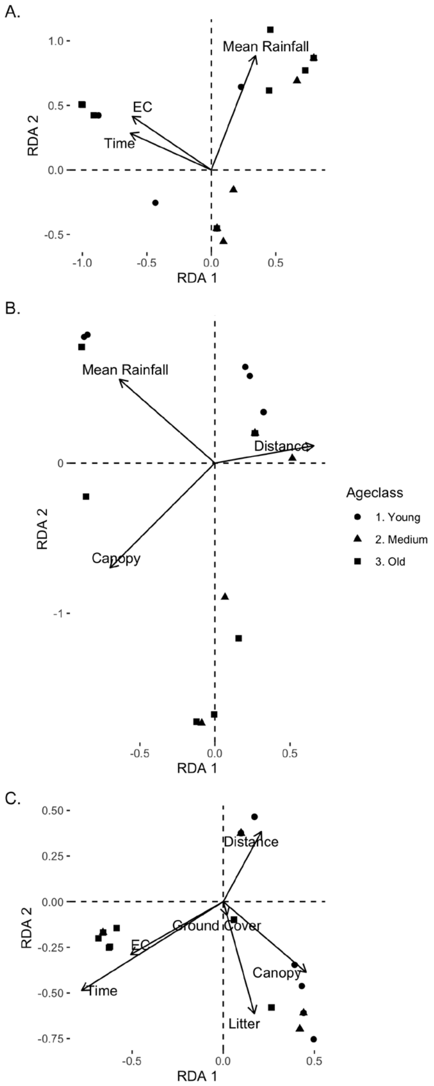
Supplementary material 1: A) tree, B) seedlings C) shrub triplots displaying how vegetation strata is influenced by different environmental variables. Scaling 2 was used for all triplots, therefore, distance between object are not approximate, however the angle between all vectors reflect linear correlation.



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