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The extent and pattern of *Eucalyptus* regeneration in an agricultural landscape

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ABSTRACT

The process of natural regeneration is critical for sustaining remnant native vegetation and the ecosystem services it supports. We quantified the extent and pattern of Eucalyptus regeneration within remnant vegetation in a fragmented agricultural landscape in south-eastern Australia. Eucalyptus regeneration was absent at 42% of sites. Using an information-theoretic approach, we explored 13 possible models of Eucalyptus regeneration across multiple scales. The explanatory variables in the four models with empirical support (and their summed Akaike weights) were: grazing intensity (1.0), native ground cover (0.99), remnant area (0.83), tenure (0.67), canopy cover (0.21) and vegetation type (0.11). Averaging across these four models we predicted that the probability of Eucalyptus regeneration was highest (0.95) in relatively unmodified remnant native vegetation, that is, remnant vegetation on public land where grazing was light and the understorey was dominated by native plants. In contrast, the predicted probability of Eucalyptus regeneration was lowest (0.12) in small remnants on private land where grazing was heavy. Our results suggest that a large proportion of all remnant native vegetation in this landscape will disappear under existing land management and farming practices. Reducing grazing pressure within intensively grazed remnants appears to be the single most effective management intervention that will mitigate this threat. This will require a shift in conservation priorities away from large, intact remnants where regeneration does not appear to be affected, to poorer quality remnants-often small remnants or scattered trees—where regeneration is typically absent.

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1. Introduction

Low levels of natural tree regeneration have been reported in agricultural and intensively grazed landscapes globally. These include *Quercus* stands in Europe (Mountford et al., 1999; Pulido et al., 2001; Plieninger et al., 2003), Asia (Saxena et al., 1984) and North America (Griffin, 1971; Palmer et al., 2004); savanna in Africa (Ben-Shahar, 1998); *Eucalyptus, Callitris* and *Allocasuarina* stands in southern Australia (Dorrough and Moxham, 2005; Maron, 2005); rainforest remnants in central America (Harvey and Haber, 1999); and *Aspidosperma* stands in South America (Barchuk and Diaz, 1999). Low levels of regeneration is a significant factor in the decline of tree cover in agricultural landscapes (Gibbons et al., 2008b).

The decline of native tree cover in agricultural landscapes is of concern because mature trees in partially cleared landscapes provide ecosystem services in quantities proportionally greater than their abundance (Manning et al., 2006). These include habitat for native species (Manning et al., 2006), salinity control (Cramer and Hobbs, 2002), a range of beneficial soil properties (Jonsson et al., 1999; Wilson, 2002) and financial benefits to farmers in terms of shelter for livestock and crops, forage for livestock, honey production, timber production and fuel wood (Harvey and Haber, 1999; Reid and Landsberg, 1999; Bentley et al., 2004; Western and Maitumo, 2004).

There is growing evidence that natural regeneration of Australia's dominant tree genus (*Eucalyptus*) is inhibited in intensively
managed agricultural landscapes (Dorrough and Moxham, 2005;
Briggs et al., 2008; Fischer et al., 2009), which is also the case for
many widespread tree genera (Griffin, 1971; Pulido et al., 2001;
Plieninger et al., 2004). Natural regeneration of *Eucalyptus* depends
on the coincidence of a proximal seed source (Dorrough and
Moxham, 2005), appropriate soil moisture and temperature (Yates
et al., 1996), the degree of harvesting by seed predators (Odowd
and Gill, 1984) and an appropriate seedbed (Faunt et al., 2006),
leading to speculation that *Eucalyptus* regeneration is naturally
episodic (Curtis, 1990). However, *Eucalyptus* regeneration has been
recored as present in virtually all relatively unmodified remnants
(Gibbons et al., 2008a), suggesting that factors associated with land

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management are the principal causes for the lack of *Eucalyptus* regeneration in agricultural landscapes. These factors are known to include cultivation, grazing by livestock and other herbivores and competition with exotic plants (Yates and Hobbs, 1997; Dorrough and Moxham, 2005; Spooner and Allcock, 2006).

An understanding of the extent and pattern of natural regeneration is critical to help land-managers, conservation agencies and governments understand the magnitude of this issue and use their limited resources to target areas where remnant native vegetation is under greatest threat. We observed natural tree regeneration in a fragmented agricultural landscape in south-eastern Australia to: (1) determine whether the proportion of remnants with natural regeneration differed to what is expected in relatively unmodified landscapes, (2) identify what parts of the landscape are at greatest threat from the lack of regeneration and (3) identify what land uses represent the greatest threat to regeneration.

2. Materials and methods

2.1. Study area

We surveyed *Eucalyptus* regeneration within, and immediately adjacent to, remnants of native vegetation over a landscape of 2577 km² in the Boorowa Shire within the Murray-Darling Basin in south-eastern Australia (34.0–34.6°S, and 148.6°–149.1°E). The climate is temperate with warm summers and cool winters (average maximum temperature is 20.7 °C and average minimum is 6.2 °C at Boorowa [weather station 070220]) and moderate rainfall (mean annual precipitation varies from 642 mm in the north [weather station 73051] to 713 mm in the southeast of the study area [weather station 70028]) (Australian Government Bureau of Meteorology, unpublished data).

Most (85%) of the woody native vegetation in the study area has been cleared for grazing by livestock (predominantly sheep and beef cattle) and cultivation since European settlement in the early 1800s (NPWS, 2002). Ridge-lines and upper slopes support dry sclerophyll forest in which red stringybark (*Eucalyptus macrorhyncha*) is usually present. Open forest and woodland dominated by red stringybark, long leaved box (*Eucalyptus goniocalyx*), and candlebark (*Eucalyptus rubida*) generally occur on sedimentary rocks of poor fertility on intermediate slopes of the study area. Box Gum Grassy Woodland dominated by white box (*Eucalyptus albens*), yellow box (*Eucalyptus melliodora*) and Blakely's red gum (*Eucalyptus blakelyi*) is widespread across the study area but occupies <10% of its pre-European extent and is listed as threatened nationally (DEH, 2006).

2.2. Sampling methodology

The study area was divided into 13 strata based on tenure (two levels), remnant size (four levels) and vegetation type (two levels) because these are broad indicators of grazing regime, native vegetation condition and environmental variation, each of which is potentially associated with *Eucalyptus* regeneration (note that three of all possible strata did not exist in the field). Stratification was undertaken using the following spatial layers: (1) a land tenure layer, derived from the NSW digital cadastral database and reclassified into two levels (public and private); (2) a vegetation community layer (NPWS, 2002) reclassified based on structural attributes into two vegetation categories (forest and woodland); and (3) a woody vegetation layer derived from a Landsat 5 multispectral image pan-sharpened with a finer-resolution ($10 \times 10 \text{ m}$) *Satellite Pour l'Observation de la Terre 4* (SPOT 4) panchromatic image (Seddon et al., 2007) classified into four remnant size classes

based on a logarithmic scale (small [0.1–1 ha], medium [1–10 ha], large [10–100 ha] and very large [>100 ha]).

Four to 16 remnants (mean = 9) were sampled within each of the 13 strata with a total of 115 remnants sampled. The boundary of each remnant was defined as the edge of the tree crown plus an additional 10 m buffer. Remnants were each sampled with 1–10 plots with larger remnants sampled with more plots because these are more heterogeneous than small remnants (i.e., larger remnants are more likely to contain >1 vegetation type, tenure, etc.). A single plot was measured in all small (n = 32) and some medium (n = 28) remnants, two plots were measured in most medium and all large (n = 39) remnants, while between six and 10 plots were measured in all very large (n = 16) remnants. Plots were typically 30×30 m (0.09 ha). A modified plot layout was used to accommodate remnants that were ≤ 30 m wide, whilst ensuring the total area surveyed (0.09 ha) remained constant. Field data were collected between lanuary and March 2005.

2.3. Dependant variable

We analysed natural Eucalyptus regeneration as a binary variable (present/absent) rather than a continuous variable (density) for the following reason. Eucalyptus regeneration occurs more-orless continuously in the vegetation types examined in this study via a process of gap-phase replacement (Florence, 1996) and is therefore virtually ubiquitous in relatively unmodified remnants (Gibbons et al., 2008a). However, relatively unmodified remnants can variously support sparse or dense regeneration depending on the history of stochastic events such as fires and floods (because Eucalyptus can regenerate profusely in these conditions) and competition from mature over-storey (because Eucalyptus are relatively intolerant to over-storey competition) (Florence, 1996). Thus, more regenerating stems does not equate with better function or better condition (i.e., the capacity of the remnant to support regeneration). We therefore considered the presence/absence of Eucalyptus regeneration was more indicative of condition than the density of regeneration, which is consistent with the approach adopted in other studies on Eucalyptus regeneration (Dorrough and Moxham, 2005; Fischer et al., 2009).

Natural *Eucalyptus* regeneration was recorded as present in a plot if at least one stem was observed. Natural *Eucalyptus* regeneration was defined as stems that were not the result of planting or artificial seeding, had a basal diameter <5 cm and were ≤300 cm tall. Minor stems in close proximity to a larger stem were only considered regeneration if greater than 20 cm distant because they were often joined below ground.

2.4. Independent variables

A number of potential explanatory variables were recorded in each 0.09 ha plot (Table 1). Some potential explanatory variables (exotic cover, native cover, bare ground, rock cover, log cover and litter cover) were not recorded across the entire plot area, but were averaged across eight, 2×2 m sub-plots established at 15 m intervals around the perimeter of each 0.09 ha plot (Table 1). Patch metrics (area, perimeter, and perimeter/area ratio) were calculated using Patch Analyst for ArcGIS (Elkie et al., 1999).

2.5. Data analyses

We explored associations between the dependent variable (presence of *Eucalyptus* regeneration) and the independent variables (Table 1) using an information-theoretic approach. First, we undertook an initial exploratory analysis to check for colinearity between potential explanatory variables (Table 1). From the remaining potential explanatory variables we identified a set of

 Table 1

 Potential explanatory variables recorded for each site.

Variable	Description
Area	Remnant area (m ²) measured using a woody vegetation layer and GIS
Perimeter	Remnant perimeter (m) measured using a woody vegetation layer and GIS
Perimeter-area ratio	Patch perimeter to area ratio
Tenure	Public tenure (crown land) or private tenure (farm land)
Vegetation type	Dominant vegetation formation derived from pooling vegetation communities: forest (dominated by red stringybark or candlebark); woodland (dominated by white box, yellow box or Blakely's red gum)
Topographic position	Predominant location in the landscape: 1. Flat; 2. Drainage line; 3. Lower slope; 4. Upper slope; 5. Ridge/crest
Grazing intensity	Visually estimated as: (1) zero (no evidence of grazing by herbivores), (2) light (no or little evidence of grazing – little herbivore dung present, few signs of disturbance by hooves, some evidence of vegetation removal), (3) moderate (signs of patch grazing, tussock structure still evident, some dung and soil disturbance present, vegetation biomass moderate), or (4) heavy (no evidence of patch grazing, no native tussocks, considerable dung and soil disturbance, vegetation biomass low and even).
Canopy cover (%)	Derived from crown separation ratio following Specht et al. (1974)
Exotic cover (%)	Visual estimate of exotic annual and perennial grass and forb cover
Native cover (%)	Visual estimate of native grasses and forbs
Bare ground (%)	Visual estimate of bare ground cover
Rock cover (%)	Visual estimate of rock cover
Log cover (%)	Visual estimate of woody debris (>5 cm diameter)
Litter cover (%)	Visual estimate of litter cover

candidate models to examine whether (a) *Eucalyptus* regeneration responds to variables reflecting fine-scale processes only, (b) variables indicative of landscape-scale processes only, or (c) variables reflecting processes at both scales.

Because our data were hierarchical or nested (149 plots were measured in 115 remnants) there was potential for dependence between plots where they were located within the same remnant. We tested for dependence by examining relationships between the probability of Eucalyptus regeneration and the explanatory variables in the candidate models using Generalised Linear Mixed Modelling (GLMM) (McCulloch et al., 2008) with a logit link implemented with the "Imer" package in R (R Development Core Team, 2010) in which a factor representing all unique remnants was fitted as a random effect to each model. In all models the variance component for the random effect representing remnants was zero suggesting no evidence for dependence. We therefore undertook all analysis of the relationships between the probability of Eucalyptus regeneration and the explanatory variables using more parsimonious Generalised Linear Models (GLM) (McCulloch et al., 2008) with a logit link using the "stats" package in R (R Development Core Team, 2010).

Each candidate model was ranked from best to worst fitting on the basis of ascending Akaike's Information Criterion (AIC) values. AIC values were transformed into AIC weights (ω) and AIC differences (Δ) (Burnham and Anderson, 2004). Akaike weights (ω_i) can be interpreted as the probability that model i is the best model, of the set, for the data (Burnham and Anderson, 2004). Models with AIC differences less than two $(\Delta_i < 2)$ have substantial empirical support and should all be considered (Burnham and Anderson, 2002). Models with substantial empirical support $(\Delta_i < 2)$ were therefore averaged using the procedure outlined in Burnham and Anderson (2002) and predictions made from this average-weighted model.

3. Results

We sampled 149 plots across 115 remnants. The frequency distribution of sampled remnant sizes was positively skewed, with sampled remnants ranging in area from 0.1 ha to 9876.4 ha with a median area of 8.6 ha. *Eucalyptus* regeneration was present in 86 of the 149 (0.09 ha) plots sampled (or 58% of plots). The percentage of plots in which regeneration was present was significantly different (χ^2 = 1533, df = 1, $p \le 0.001$) to the percentage of

plots (97%) expected to contain *Eucalyptus* regeneration in these vegetation types (Gibbons et al., 2008a).

3.1. Variables associated with natural regeneration

The log of remnant area was highly correlated with perimeter (r = 0.73) and perimeter to area ratio (r = -0.82). The latter two variables were removed from further analysis as the area of a remnant is the easiest of the three variables to interpret. From the remaining explanatory variables we identified ten potential GLMs predicting the probability of natural regeneration (Table 2) based on what we considered to be the key site and landscape variables that are likely to affect regeneration and are informative to landmanagers. In each of the models containing grazing intensity there were no significant differences between several levels of this factor. This variable was therefore collapsed from the original four levels that were recorded in the field (see Table 1) to two levels as follows: zero, light and moderate grazing = 'light' grazing; and heavy grazing = 'heavy' grazing.

Akaike weights and evidence ratios suggested that four of the 13 candidate models had strong support (Akaike difference < 2) (Table 2). The summed Akaike weights from the 13 candidate models indicated that the most influential variables affecting *Eucalyptus* regeneration in descending order were: grazing intensity (1.00), native cover (0.99), remnant area (0.83), tenure (0.67),

Table 2 Candidate models for natural regeneration that were examined and their associated AIC, AIC differences (Δ_i) and Akaike weights (ω_i) . Models with empirical support $(\Delta_i < 2)$ are in bold $(G = \text{grazing intensity}, N = \text{native understorey cover}, C = \text{canopy cover}, B = \text{bare ground}, T = \text{land tenure}, A = \log_{10}(\text{remnant area}), V = \text{vegetation type}).$

Model	AIC	Δ_i	ω_i
G	179.99	7.69	0.01
G + N	175.70	3.40	0.05
G + N + C	177.50	5.20	0.02
G + N + C + B	179.49	7.19	0.01
T	197.07	24.77	0.00
T + A	188.73	16.43	0.00
T + A + V	190.73	18.43	0.00
G + N + T	174.85	2.55	0.08
G + N + A	172.73	0.43	0.24
G + N + T + A	172.30	0	0.30
G + N + T + A + V	174.22	1.92	0.11
G + N + C + T + A	173.97	1.67	0.13
G + N + C + B + T + A	175.87	3.57	0.05

canopy cover (0.21) and vegetation type (0.11). Each of grazing intensity, native cover and remnant area occurred in the four models with strong support (Table 2).

3.2. Predictions from an average-weighted model

An average-weighted model (across the four models with strong support) contained the explanatory variables grazing intensity, native understorey cover, tenure, remnant area (\log_{10}) vegetation type and canopy (Table 3). Predictions for each of the significant explanatory variables in the average-weighted model (with other significant explanatory variables held at reference levels) are illustrated in Fig. 1. In an averaged-sized remnant, the mean proportion of sites with regeneration decreased from 0.95 on public land where grazing was 'light' and the understorey was totally native to 0.14 on private land where grazing was 'heavy' and the understorey was totally exotic. In remnants with average native understorey cover, the mean proportion of sites with regeneration decreased from 0.84 in large remnants (10,000 ha) on public land where grazing was 'light' to 0.12 in small remnants (0.1 ha) on private land where grazing was 'heavy'. Other things equal, predictions from the average-weighted model suggested that regeneration, on average, was less likely to be present in woodland relative to forest and was negatively associated with canopy cover. However, these two relationships are extremely weak as indicated by the low parameter estimate and/or high standard error around this estimate for these variables (Table 3).

4. Discussion

4.1. Is there a tree regeneration problem in agricultural landscapes?

Our study adds to a body of evidence that over-storey regeneration is restricted in agricultural landscapes. In this study Eucalyptus regeneration was present at 58% of sampled sites. Other studies in agricultural landscapes have reported similar results. For example, in an agricultural landscape dominated by Eucalyptus species south of our study area Dorrough and Moxham (2005) found that 27% of sites they surveyed (including sites without remnant vegetation) contained regeneration. In a review of landscapes dominated by Quercus lobata in North America 45% of sites contained regeneration (Zavaleta et al., 2007). Quercus regeneration in Spanish dehesas was 2% of the density of regeneration in comparable forest (Pulido et al., 2001). Tree regeneration can be naturally episodic because of the range of conditions that must be coincident for it to occur (Barnes, 1983; Barchuk and Diaz, 1999), so do our observations that regeneration occurred at 58% of sites represent a deviation from the expected pattern of natural tree regeneration for *Eucalyptus* in this landscape?

Our results suggest the answer to this question is "yes". The per cent of sites that we observed regeneration (58%) was significantly

Table 3Parameter estimates and standard errors (SEs) for the average-weighted model of natural regeneration of eucalypts.

Term	Estimate	SE
Intercept	-1.66	0.89
Grazing intensity 'light'	0	_
Grazing intensity 'heavy'	-2.22	0.80
% Native understorey cover	0.03	0.02
Land tenure 'private'	0	_
Land tenure 'public'	0.69	0.44
Remnant area (log ₁₀)	0.30	0.14
Vegetation 'forest'	0	_
Vegetation 'woodland'	-0.13	0.47
Canopy	-0.01	0.02

different to the per cent of sites expected to contain regeneration (97%), in a study of comparable, but relatively unmodified, sites by Gibbons et al. (2008a). Further, the predicted proportion of relatively unmodified remnants (i.e., remnants on public land with a predominantly native understorey) that contained regeneration (0.95) was considerably higher than the predicted proportion of sites that contained regeneration on private land where grazing was heavy and either the understorey was exotic (0.14) or the remnant small (0.12). These results support the suggestion that these ecosystems naturally regenerate via a process of continual gapphase replacement (Florence, 1996) and *Eucalyptus* regeneration is inhibited where agricultural activities are intensive.

4.2. Land use and landscape factors associated with the pattern of tree regeneration

Of the measured variables, grazing intensity was the primary factor affecting Eucalyptus regeneration, with no empirical support for models that did not include this variable (models not containing this variable had AIC differences $[\Delta_i] > 16$). This finding is replicated across agricultural landscapes globally (reviewed by Manning et al. (2006)). High grazing intensity is likely to inhibit regeneration directly via at least two mechanisms: (1) germination is inhibited from modifications to the seedbed and (2) the survival of seedlings is compromised from browsing pressure. Several environmental conditions that can be affected by grazing must be met for a Eucalyptus seed to germinate. Eucalyptus seed lacks an endosperm and does not persist in the soil, but is released from the canopy when conditions are likely to be suitable for germination (Florence, 1996). While it is believed that eucalypts require exposed mineral soil to germinate (Jacobs, 1955), an exposed seedbed that is also compacted by livestock (a major herbivore in this landscape) can be hostile to germination (Yates et al., 1996; Pettit and Froend, 2001). If Eucalyptus seed germinates then it can be affected by browsing. In our study area potential browsers of young Eucalyptus foliage include invertebrates (Landsberg et al., 1990). livestock (Dorrough et al., 2004), some native vertebrates such as the swamp wallaby (Wallabia bicolor) (Di Stefano et al., 2007) and introduced rabbits and hares (Saunders et al., 2003).

We recorded no significant differences in the proportion of sites with regeneration between sites that we classified as 'zero', 'light' and 'moderate' grazing intensity (see definitions in Table 1). This is consistent with several studies in which natural Eucalyptus regeneration was observed in the presence of intermittent periods of heavy grazing by livestock between periods of no grazing or light grazing (Curtis and Wright, 1993; Spooner et al., 2002; Briggs et al., 2008; Fischer et al., 2009)—an observation that has also been made for other tree genera (Hester et al., 1996; Pulido et al., 2001). These observations are further supported by the patterns of regeneration that we observed in different land tenures. Remnant native vegetation on private land in the study area is more likely to have a history of continuous grazing by livestock, while grazing by livestock in public land within the study area (roadsides and travelling stock reserves) is typically intermittent or has been absent for a long period (Prober and Thiele, 1995; Dorrough and Moxham, 2005). Land tenure was a significant explanatory variable in three of the four best regression models with public land, on average, having a greater probability of supporting natural Eucalyptus regeneration than private land (Fig. 1).

Eucalyptus regeneration was positively associated with the per cent of native understorey cover in each of the four models with empirical support (Table 2) and the average-weighted model (Table 3). This result is consistent with other studies (Cluff and Semple, 1994; Li et al., 2003; Dorrough and Moxham, 2005). This result may be indirectly linked to grazing pressure. Although native understorey cover and grazing intensity were not highly

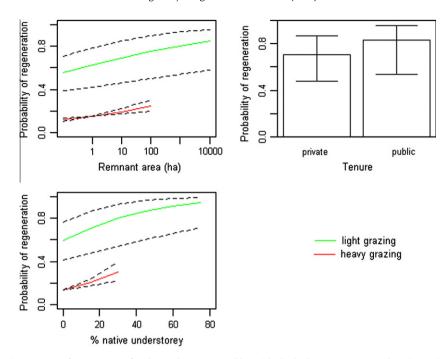


Fig. 1. Predicted probabilities (mean \pm SE) of regeneration for the explanatory variables with the highest importance values (\geqslant 0.67) in the average-weighted model. Predictions for the variables remnant area (\log_{10}) and per cent understorey cover were made with the other continuous variable fixed at their mean, tenure fixed at 'private' and vegetation fixed at 'woodland'. The prediction for the variable tenure was made with the other continuous variables held at their mean, grazing fixed at 'light' and vegetation fixed at 'woodland'.

correlated, sites that were intensively grazed did not support high native understorey cover (Fig. 1). Intensive grazing by livestock is associated with pasture improvement, which involves soil disturbance, the introduction of exotic pasture species and the use of superphosphate. These actions all affect natural regeneration (Fischer et al., 2009).

Remnant area was a significant explanatory variable in the four best models (Table 2), with the probability of regeneration lowest in smaller remnants (Fig. 1). Remnant area was correlated with remnant perimeter and perimeter to area ratio. The effects of small remnants, remnants with a long perimeter or remnants with a high perimeter to area ratio include: loss of genetic vigour from reduced out-crossing (Burrows, 2000), increased susceptibility to the effects of grazing and invasion by exotic plants (McIntyre and Lavorel, 1994) and influxes of nutrients from surrounding land uses (Yates and Hobbs, 1997).

Seedlings of many tree species, including each Eucalyptus species observed in this study, form lignotubers. Lignotubers enable seedlings to resprout after perturbations such as drought, grazing or fire. Lignotuberous seedlings of the genus Eucalyptus can potentially persist for decades when conditions are not suitable for growth (e.g., because of over-storey competition) (Noble, 1984). Survival of Eucalyptus seedlings from fire was positively associated with the size of the lignotuber (Noble, 1984). We did not measure the size of lignotubers in this study. However, it is feasible that the size of the lignotuber (or the age of the seedling) is an important factor affecting seedling persistence which was not examined in this study. Further, if the ability of a seedling to survive perturbations such as grazing is affected by the size of the lignotuber, then sites in which seedlings with lignotubers no longer persist (e.g., due to a history of grazing or soil disturbance), may be more difficult to regenerate naturally because they can only regenerate from seed. Pulido et al. (2001) noted that Holm oak (Quercus ilex) regeneration in agricultural landscapes in Spain only occurred vegetatively, suggesting that regeneration from seed was not possible under conditions of intensive grazing by livestock.

4.3. The importance of small, modified remnants for conservation in agricultural landscapes

Our results illustrate that modified and/or small remnants can be important conservation priorities in fragmented agricultural landscapes. Governments invest considerably in conservation actions within agricultural landscapes via agri-environmental schemes (Ribaudo et al., 2001; Kleijn et al., 2006). In these schemes conservation priorities in remnant native vegetation are often set according to condition or quality (e.g., proximity of a site to reference conditions, the number of species on a site) and/or irreplaceability (the importance of a site for meeting a conservation target) (Pressey and Bottrill, 2008), with the total area protected often used as the metric to summarise conservation achievement. Our study demonstrates that this can be a dangerous strategy for prioritising conservation investment in these landscapes. In our study area this strategy would place a priority on the conservation of large patches of woodland vegetation on public land as these are the remnants that are in best condition and with highest irreplaceability (sensu Pressey and Bottrill, 2008). However, our results suggest that this conservation strategy would result in considerable loss of remnant native vegetation. This is because large remnants on public land are at relatively low threat of decline from lack of regeneration (Fig. 1). Similarly, these remnants cannot generally be cleared under native vegetation laws in Australia, tend to have relatively low cover of exotic plants and are generally not available for intensive grazing. Conversely, small and/or modified remnants on private land are at considerable risk of further decline without a change in management. This is because these remnants have relatively low probabilities of containing regeneration (Fig. 1), tend to have higher exotic plant cover, are more likely to be intensively grazed and can be cleared under some circumstances (Gibbons et al., 2009). Further, Gibbons et al. (2008b) found that tree cover is on a steep trajectory of decline in highly modified stands in agricultural landscapes, but this can be ameliorated with management intervention. Thus, conservation efforts on large, intact remnants

are unlikely to result in much improvement in conservation values within these landscapes relative to small and/or highly modified remnants that have the highest likelihood of loss under the status quo.

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References

- Barchuk, A.H., Diaz, M.D., 1999. Regeneration and structure of *Aspidosperma quebracho-blanco* Schl. in the Arid Chaco (Cordoba, Argentina). Forest Ecology and Management 118, 31–36.
- Barnes, R.F.W., 1983. Effects of elephant browsing on woodlands in a Tanzanian National Park measurements, models and management. Journal of Applied Ecology 20, 521–539.
- Ben-Shahar, R., 1998. Changes in structure of savanna woodlands in northern Botswana following the impacts of elephants and fire. Plant Ecology 136, 189– 194
- Bentley, J.W., Boa, E., Stonehouse, J., 2004. Neighbor trees: shade, intercropping and cacao in Equador. Human Ecology 32.
- Briggs, S.V., Taws, N.M., Seddon, J.A., Vanzella, B., 2008. Condition of fenced and unfenced remnant vegetation in inland catchments in south-eastern Australia. Australian lournal of Botany 56, 590–599.
- Australian Journal of Botany 56, 590–599.

 Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical-Theoretic Approach, second ed. Springer-Verlag, New York.
- Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods Research 33, 261–304.
- Burrows, G.E., 2000. Seed production in woodland and isolated trees of *Eucalyptus melliodora* (yellow box, Myrtaceae) in the south western slopes of New South Wales. Australian Journal of Botany 48, 681–685.
- Cluff, D., Semple, B., 1994. Natural regeneration in "Mother Nature's" own time. Australian Journal of Soil and Water Conservation 7, 28–33.
- Cramer, V.A., Hobbs, R.J., 2002. Ecological consequences of altered hydrological regimes in fragmented ecosystems in southern Australia: impacts and possible management responses. Austral Ecology 27, 546–564.
- Curtis, D., 1990. Natural regeneration of eucalypts in the New England region. In: Sowing the Seeds, Proceedings of a Direct Seeding and Natural Regeneration Conference, Greening Australia, Adelaide, pp. 7–16.
- Curtis, D., Wright, T., 1993. Natural regeneration and grazing management a case study. Australian Journal of Soil and Water Conservation 6, 30–34.
- DEH, 2006. Advice to the Minister for the Environment and Heritage from the Threatened Species Scientific Committee (TSSC) on Amendments to the List of Ecological Communities under the Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act), Department of the Environment and Heritage, Canberra.
- Di Stefano, J., Anson, J.A., York, A., Greenfield, A., Coulson, G., Berman, A., Bladen, M., 2007. Interactions between timber harvesting and swamp wallabies (Wallabia bicolor): space use, density and browsing impact. Forest Ecology and Management 253, 128–137.
- Dorrough, J., Ash, J., McIntyre, S., 2004. Plant responses to livestock grazing frequency in an Australian temperate grassland. Ecography 27, 798–810.
- Dorrough, J., Moxham, C., 2005. Eucalypt establishment in agricultural landscapes and implications for landscape-scale restoration. Biological Conservation 123, 55–66
- Elkie, P.C., Rempel, R.S., Carr, A.P., 1999. Patch Analyst Users Manual: A Tool for Quantifying Landscape Structure. Ontario Ministry of Natural Resources Northwest Science and Technology, Ontario.
- Faunt, K., Geary, P., Cunningham, R.B., Gibbons, P., 2006. The East Gippsland silvicultural systems project. II: germination and early survival of eucalypt regeneration. Australian Forestry 69, 182–197.
- Fischer, J., Stott, J., Zerger, A., Warren, G., Sherren, K., Forrester, R.I., 2009. Reversing a tree regeneration crisis in an endangered ecoregion. Proceedings of the National Academy of Sciences of the United States of America 106, 10386–10391.
- Florence, R.G., 1996. Ecology and Silviculture of Eucalypt Forests. CSIRO Publishing, Collingwood.
- Gibbons, P., Briggs, S.V., Ayers, D.A., Doyle, S., Seddon, J., McElhinny, C., Jones, N., Sims, R., Doody, J.S., 2008a. Rapidly quantifying reference conditions in modified landscapes. Biological Conservation 141, 2483–2493.

- Gibbons, P., Briggs, S.V., Ayers, D.A., Seddon, J.A., Doyle, S.J., Cosier, P., McElhinny, C., Pelly, V., Roberts, K., 2009. An operational method to assess impacts of land clearing on terrestrial biodiversity. Ecological Indicators 9, 26–40.
- Gibbons, P., Lindenmayer, D.B., Fischer, J., Manning, A.D., Weinberg, A., Seddon, J., Ryan, P., Barrett, G., 2008b. The future of scattered trees in agricultural landscapes. Conservation Biology 22, 1309–1319.
- Griffin, J.R., 1971. Oak regeneration in upper Carmel Valley, California. Ecology 52, 862–868.
- Harvey, C.A., Haber, W.A., 1999. Remnant trees and the conservation of biodiversity in Costa Rican pastures. Agroforestry Systems 44, 37–68.
- Hester, A.J., Mitchell, F.J.G., Kirby, K.J., 1996. Effects of season and intensity of sheep grazing on tree regeneration in a British upland woodland. Forest Ecology and Management 88, 99–106.
- Jacobs, M.R., 1955. Growth Habits of the Eucalypts. Forestry and Timber Bureau, Canberra.
- Jonsson, K., Ong, C.K., Odongo, J.C.W., 1999. Influence of scattered nere and karite trees on microclimate, soil fertility and millet yield in Burkina Faso. Experimental Agriculture 35, 39–53.
- Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M., Yela, J.L., 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecology Letters 9, 243–254.
- Landsberg, J., Morse, J., Khanna, P., 1990. Tree dieback and insect dynamics in remnants of native woodlands on farms. Proceedings of the Ecological Society of Australia 16, 149–165.
- Li, J., Duggin, J.A., Grant, C.D., Loneragan, W.A., 2003. Germination and early survival of *Eucalyptus blakelyi* in grasslands of the New England Tablelands, NSW, Australia. Forest Ecology and Management 173, 319–334.
- Manning, A.D., Fischer, J., Lindenmayer, D.B., 2006. Scattered trees are keystone structures implications for conservation. Biological Conservation 132, 311–321.
- Maron, M., 2005. Agricultural change and paddock tree loss: implications for an endangered subspecies of Red-tailed Black-Cockatoo. Ecological Management and Restoration 6, 207–212.
- McCulloch, C.E., Searle, S.R., Neuhaus, J.M., 2008. Generalized, Linear, and Mixed Models. John Wiley and Sons, New York.
- McIntyre, S., Lavorel, S., 1994. How environmental and disturbance factors influence species composition in temperate Australian grasslands. Journal of Vegetation Science 5, 373–384.
- Mountford, E.P., Peterken, G.F., Edwards, P.J., Manners, J.G., 1999. Long-term change in growth, mortality and regeneration of trees in Denny Wood, an old-growth wood-pasture in the New Forest (UK). Perspectives in Plant Ecology, Evolution and Systematics 2, 223–272.
- Noble, I.R., 1984. Mortality of lignotuberous seedlings of *Eucalyptus* species after an intense fire in montane forest. Austral Ecology 9, 47–50.
- NPWS, 2002. The Native Vegetation of Boorowa Shire. National Parks and Wildlife Service. Queanbeyan.
- Odowd, D.J., Gill, A.M., 1984. Predator satiation and site alteration following fire mass reproduction of Alpine Ash (*Eucalyptus delegatensis*) in southeastern Australia. Ecology 65, 1052–1066.
- Palmer, S.C.F., Mitchell, R.J., Truscott, A.M., Welch, D., 2004. Regeneration failure in Atlantic oakwoods: the roles of ungulate grazing and invertebrates. Forest Ecology and Management 192, 251–265.
- Pettit, N.E., Froend, R.H., 2001. Long-term changes in the vegetation after the cessation of livestock grazing in *Eucalyptus marginata* (jarrah) woodland remnants. Austral Ecology 26, 22–31.
- Plieninger, T., Pulido, F.J., Konold, W., 2003. Effects of land-use history on size structure of holm oak stands in Spanish dehesas: implications for conservation and restoration. Environmental Conservation 30, 61–70.
- Plieninger, T., Pulido, F.J., Schaich, H., 2004. Effects of land-use and landscape structure on holm oak recruitment and regeneration at farm level in *Quercus ilex* L. Dehesas. Journal of Arid Environments 57, 345–364.
- Pressey, R.L., Bottrill, M., 2008. Opportunism, threats and the evolution of systematic conservation planning. Conservation Biology 22, 1340–1345.
- Prober, S.M., Thiele, K.R., 1995. Conservation of the grassy white box woodlands: relative contributions of size and disturbance to floristic composition and diversity of remnants. Australian Journal of Botany 43, 349–366.
- Pulido, F.J., Diaz, M., de Trucios, S.J.H., 2001. Size structure and regeneration of Spanish holm oak Quercus ilex forests and dehesas: effects of agroforestry use on their long-term sustainability. Forest Ecology and Management 146, 1–13.
- R Development Core Team, 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reid, N., Landsberg, J., 1999. Tree decline in agricultural landscapes: what we stand to lose. In: Hobbs, R.J., Yates, C.J. (Eds.), Temperate Eucalypt Woodlands in Australia: Biology, Conservation, Management and Restoration. Surrey Beatty and Sons, Chipping Norton, pp. 127–166.
- Ribaudo, M.O., Hoag, D.L., Smith, M.E., Heimlich, R., 2001. Environmental indices and the politics of the Conservation Reserve Program. Ecological Indicators 1, 11–20
- Saunders, D.A., Smith, G.T., Ingram, J.A., Forrester, R.I., 2003. Changes in a remnant of salmon gum *Eucalyptus salmonophloia* and York gum *E. loxophleba* woodland, 1978 to 1997. Implications for woodland conservation in the wheat-sheep regions of Australia. Biological Conservation 110, 245–256.
- Saxena, A.K., Singh, S.P., Singh, J.S., 1984. Population structure of forests of Kumaun Himalaya: implications for management. Journal of Environmental Management 19, 307–324.

- Seddon, J.A., Zerger, A., Doyle, S.J., Briggs, S.V., 2007. The extent of dryland salinity in remnant woodland and forest within an agricultural landscape. Australian Journal of Botany 55, 533–540.
- Specht, R.L., Roe, M.E., Broughton, V.H., 1974. Conservation of major plant communities in Australia and Papua New Guinea. Australian Journal of Botany Supplement 1, 667.
- Spooner, P., Lunt, I., Robinson, W., 2002. Is fencing enough? The short-term effects of stock exclusion in remnant grassy woodlands in southern NSW. Ecological Management and Restoration 3, 117–126.
- Spooner, P.G., Allcock, K.G., 2006. Using a state and transition approach to manage endangered *Eucalyptus albens* (white box) woodlands. Environmental Management 38, 771–783.
- Western, D., Maitumo, D., 2004. Woodland loss and restoration in a savanna park: a 20-year experiment. African Journal of Ecology 42, 111–121.
- Wilson, B., 2002. Influence of scattered paddock trees on surface soil properties: a study of the Northern Tablelands of NSW. Ecological Management and Restoration 3, 211–219.
- Yates, C.J., Hobbs, R.J., 1997. Temperate eucalypt woodlands: a review of their status, processes threatening their persistence and techniques for restoration. Australian Journal of Botany 45, 949–973.
- Yates, C.J., Hobbs, R.J., Bell, R.W., 1996. Factors limiting the recruitment of Eucalyptus salmonophloia in remnant woodlands. 3. Conditions necessary for seed germination. Australian Journal of Botany 44, 283–296.
- Zavaleta, E.S., Hulvey, K.B., Fulfrost, B., 2007. Regional patterns of recruitment success and failure in two endemic California oaks. Diversity and Distributions 13, 735–745.