Natural tree regeneration in agricultural landscapes: The implications of intensification

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ABSTRACT

Concern about food security is prompting a push to intensify agriculture globally. However, agricultural intensification can inhibit regeneration of vegetation in natural ecosystems. This may jeopardise the persistence of trees in agricultural landscapes and the ecosystem services these treed landscapes offer. Here, we study one of the world's most altered ecosystems – temperate eucalypt woodlands – to explore patterns in natural regeneration of trees, and factors influencing regeneration occurrence, across 300 000 km^2 of south-eastern Australia between 2008 and 2014. During this period, we found the proportion of remnants supporting natural regeneration was stable, and that regeneration occurrence was negatively associated with variables coincident with agricultural intensification: continuous livestock grazing by sheep and cattle, increased exotic plant cover, increased natural soil fertility, and lower elevation. These results indicate that intensive agriculture is incompatible with natural regeneration in our study area. Left unaddressed, low levels of regeneration may result in the widespread loss of trees and the ecosystem services they provide in agricultural landscapes. Thus, strategic implementation of land-sparing and land-sharing strategies is required across broad spatial scales to satisfy production and conservation needs. Based on our results, we recommend that land sharing be prioritised where: (1) livestock grazing can be removed or employed intermittently, (2) exotic plants do not dominate the ground layer, and (3) natural soil fertility is low. For locations that are continuously grazed or dominated by exotic plants, a land-sparing strategy may be more appropriate. Here, farmland should be managed to maximise production, and the next generation of trees should be 'moved' to areas where natural regeneration can be supported.

KEYWORDS: agri-environment schemes; agricultural landscapes; livestock grazing; *Eucalyptus*; restoration; woodland

1. INTRODUCTION

By 2050, the global human population is estimated to reach 9.6 billion (UN, 2013). To meet the food demands for a population of this size, worldwide agricultural production will need to increase by 70% (Alexandratos and Bruinsma, 2012). Agricultural expansion and intensification (i.e. means by which production gains are made using increased inputs per unit land area; Tilman et al., 2011) are strategies that can be used to meet this demand (Cunningham et al., 2013; Godfray et al., 2010) and have served to increase agricultural yields and total production in the past (Nellemann et al., 2009). However, agricultural expansion and intensification can degrade ecosystems by reducing water quality (e.g. through nitrogen and phosphorous-driven eutrophication; Tilman et al., 2001), exhausting soil nutrients (Matson et al., 1997) and reducing the ability for native vegetation to regenerate naturally (Dorrough and Moxham, 2005; Weinberg et al., 2011).

Natural regeneration (i.e. the establishment of young trees from seed; Dorrough and Moxham, 2005) is critical because it supplies landscapes with the next generation of trees as well as the ecosystem services they offer. The conservation value of scattered paddock trees compared to native remnant vegetation is disputed by some agencies (e.g. there is a movement away from protecting scattered paddock trees under the *Native Vegetation Regulation 2013* in New South Wales, Australia). However, in agricultural landscapes where scattered paddock trees comprise a large proportion of total tree cover (e.g. south-eastern Australia; Gibbons and Boak, 2002), the value of scattered trees (in terms of the services they provide) is disproportionately high (Fischer et al., 2010; Manning et al., 2006). In agricultural landscapes, the services provided by native trees include: (1) provision of essential habitat for fauna (e.g. hollows for obligate hollow nesters; Manning et al., 2013), (2) supporting insect pollinators (Lentini et al., 2012), (3) maintaining or improving soil quality (e.g. increasing water retention capacity; Jonsson et al., 1999; controlling erosion; Plieninger et al., 2004;

buffering salinity; Reid et al., 2000; buffering acidity; Wilson, 2002), (4) provision of wind protection for crops (Bird et al., 1992), and (5) provision of shade for stock and crops (Bentley et al., 2004; Reid et al., 2000). Given the benefits derived from the continued presence of trees in agricultural landscapes, understanding the regeneration niche (as described by Grubb, 1977) and factors that influence tree regeneration is essential for determining whether an ecosystem will persist or potentially collapse.

Factors influencing tree regeneration in agricultural landscapes are well researched – particularly the effects of land-use history and current grazing regimes (Carmona et al., 2013; Fischer et al., 2009; Weinberg et al., 2011). This research has informed, and continues to inform, attempts to restore and revegetate degraded agricultural ecosystems through regional-scale agri-environment schemes in Europe (Environmental Stewardship Program in UK; DEFRA, 2014; Ecological Compensation Areas in Switzerland; Kleijn et al., 2006), North America (Conservation Stewardship Program; USDA, 2014) and Australia (Environmental Stewardship Program; Lindenmayer et al., 2012; Biodiversity Baseline Monitoring Program; Michael et al., 2014). However, despite the growing body of literature regarding tree regeneration, the occurrence and extent of regeneration across broad spatiotemporal scales is poorly understood, making effective management for biodiversity conservation challenging.

In this paper, we address this issue using temperate eucalypt woodlands - a critically endangered ecosystem in Australia (TSSC, 2015) – in agricultural landscapes as a focal study system. Since European settlement, almost 90% of Australian temperate eucalypt woodlands have been cleared for agricultural purposes (Kabii and Horwitz, 2006), and remaining woodland remnants are often degraded (Yates and Hobbs, 1997). These remnants represent a significant proportion of the global extent of this biome (Hoekstra et al., 2005), but face the continued threat of degradation from agricultural activities (particularly agricultural intensification; McIntyre, 2012). To better understand and manage regeneration in temperate eucalypt woodlands, we use - for the first time - empirical data of eucalypt regeneration spanning a six year period, four study regions and a vast agricultural area (approximately 300 000 km^2) in south-eastern Australia to answer two questions, (1) Is the spatial extent of natural regeneration declining through time in agricultural landscapes in different bioclimatic regions? and (2) Across broad spatial scales, are there consistent site-level and landscape-scale factors associated with natural regeneration in agricultural landscapes?

First, we postulate that over time, there will be a decline in the number of sites supporting natural regeneration as predicted by Vesk and Dorrough (2006) and Fischer et al. (2009; 2010). Second, we postulate that a combination of site-level and broad-scale factors will be associated with natural regeneration. We expect that continuous livestock grazing (Carmona et al., 2013; Weinberg et al., 2011), cover of exotic plants (Gibbons et al., 2008b; Meiners, 2007) and soil fertility (Dorrough and Scroggie, 2008; Skinner et al., 2010) will have consistent negative associations with regeneration across broad spatiotemporal scales, given the marked effect these factors have in regional and snapshot regeneration studies. We also expect that factors such as elevation (Curtis, 1990), and cover and richness of native plant species (Spooner et al., 2002; Weinberg et al., 2011) will have positive associations with regeneration, consistent with previous research.

Our results provide important new information about contemporary patterns in natural regeneration in agricultural systems. Our results also provide new perspectives on where and when to prioritize landscapes for land-sharing (associated with extensive farming) or land-sparing strategies (associated with intensive farming; Fischer et al., 2014; Green et al., 2005; Norris, 2008) across broad spatial scales, using factors associated with natural regeneration as key criteria in the decision-making process.

2. METHODS

2.1 Study Region

We examined quantitative data on regeneration in four broad-scale, medium-term studies in south-eastern Australia: Biodiversity Baseline Monitoring Program (‘BBMP’; Michael et al., 2014), South-west Slopes restoration study (‘SWS’; Cunningham et al., 2007), Nanangroe study (‘Nanangroe’; Lindenmayer et al., 2001), Environmental Stewardship Program (‘Stewardship’; Lindenmayer et al., 2012) (Fig. 1). The area covered by the four study regions is approximately 300 000 km^2. All four studies were located in landscapes with a land-use history dominated by livestock (predominantly cattle and sheep) grazing and cropping (predominantly wheat). Grazing pastures may be modified (e.g. fertilized or fertilized and oversown with exotic forage plants to increase productivity) or unmodified (e.g. no intentional fertilizer and/or exotic forage plant addition) native grasslands (Dear and Ewing, 2008). Prior to European settlement, the study regions would have been largely covered by temperate woodlands (Lindenmayer et al., 2010; Yates and Hobbs, 1997). Remaining woodland remnants are largely embedded within an agricultural matrix and are dominated, or were previously dominated, by a variety of *Eucalyptus* and *Callitris* tree species (Yates and Hobbs, 1997). The understorey of more intact remnants contains a species-rich mix of tussock grasses, herbs and scattered shrubs (TSSC, 2015; Yates and Hobbs, 1997). In relatively unmodified examples of these remnants, the occurrence of natural regeneration is the norm (e.g. between 90 – 100 % of remnants support natural regeneration; Gibbons et al., 2008a). For a detailed description of each study, see Appendix A.

2.2 Data Collection

Our investigation comprised 662 remnant woodland sites across four studies (BBMP: n = 105, SWS: n = 138, Nanangroe: n = 111, Stewardship: n = 308) in New South Wales, Australia. We established all sites in eucalypt woodland remnants that ranged in size from <1 ha to 150 ha. At all sites, we collected a consistent set of site-level vegetation attributes (see Table A.1) along a permanent 200 m transect. We measured percentage cover of ground layer native and exotic plants, bare ground, soil crust, leaf litter, overstorey and mid-storey along two 50 m sections of the transect between 0 – 50 m and 150 – 200 m, using the point-intercept method (Goodall, 1952). We measured native plant species richness within a 20 x 20 m plot centred on the 100 m point of the transect, and structural vegetation attributes – including total length of fallen logs and measures of natural eucalypt regeneration (i.e. eucalypt seedling abundance, proportion of overstorey eucalypt species present as seedlings/saplings) – within two 50 x 20 m plots located at either end of the transect. For the SWS, we measured natural regeneration in three 20 x 20 m plots, recording the mean percent understorey cover of eucalypts across the three plots. We assigned an approximate grazing intensity level to each site based on field observations of the frequency of grazing across a three-year period. The three categories we used were: no grazing (< 7 days of lightly stocked grazing per year, where lightly stocked grazing is equivalent to less than seven dry sheep equivalent [DSE] ha^{-1}), intermittent grazing (≤ 6 months total grazing per year with varying levels of stocking, predominantly less than three DSE ha^{-1} but in some cases up to 40 DSE ha^{-1}), and continuous grazing (> 6 months grazing per year with varying levels of stocking, predominantly less than eight DSE ha^{-1} but up to 30 DSE ha^{-1}). The geographic spread of sites meant that our study encompassed a wide range of grazing practices (in response to different climate, soils etc.) making it difficult to place fixed numbers on the grazing categories. As such, these categories should instead be seen as relative to local contexts. To each site, we also assigned a Keith Class (a vegetation classification based on floristic, structural and ecological features; *sensu* Keith, 2004) based on field observations (allowing us to investigate whether differences in regeneration rates may be due to dominant eucalypt species). For a complete list of site-level attributes collected, see Table A.1.

We also obtained landscape-scale environmental descriptors (including elevation, aspect, topographic wetness index (TWI), accumulated runoff, natural soil fertility, and native woody vegetation cover in a 250 m buffer around the site) and weather variables (including two-year mean annual maximum temperature, two-year mean annual precipitation, two-year mean seasonal precipitation and plant growth index) for each site. We explored alternate time lags in eucalypt regeneration responses by including one-year, two-year and five-year weather means. Our analyses revealed no significant difference in model fit among the different lag periods (ΔAIC < 2). All results presented here are based on eucalypt responses to two-year weather means as these models had the lowest AIC values. For a complete list of landscape-level and weather attributes and their definitions, see Table A.2.

2.3 Statistical Analysis

For all 662 sites in our study, we aggregated data across plots to obtain site-level estimates for all variables for each year of observation. We converted eucalypt regeneration measures to a binary variable (presence/absence) to ensure consistency in the response variable between studies, and because the presence of regeneration (rather than abundance or density) is more indicative of remnant condition, hence the *capacity* of a site to support regeneration (Weinberg et al., 2011). For all analyses (spatial and temporal), we included only those sites with response variable data (i.e. presence/absence of eucalypt regeneration) available for every year of analysis (see Table A.3) that were located within the Riverina, New South Wales South-west Slopes and South-eastern Highlands Interim Biogeographic Regionalisation for Australia (IBRA) bioregions (Australian Government, 2013). Additionally, for temporal analyses, we included only sites where data were collected in multiple years (e.g. data for Nanangroe were only available for 2010, so we excluded them from trend analyses). Thus, in total, we retained 353 sites for temporal analyses (BBMP: n =

84, SWS: n = 73, Stewardship: n = 196) and 463 sites for spatial analyses (BBMP: n = 84, SWS: n = 73, Nanangroe: n = 110, Stewardship: n = 196).

2.3.1 Are rates of regeneration declining through time?

To investigate whether the proportion of sites supporting eucalypt regeneration changed over time in different bioclimatic regions, we fitted individual generalised linear mixed models (GLMM; Bolker et al., 2009) for each study with two or more years of repeat surveys. For each model, we assumed a Bernoulli distribution with a logit-link function for the response variable (regeneration presence), and fitted Year and IBRA subregion as fixed effects and Site as a random effect. We assessed the significance of each variable within the model using Wald tests.

2.3.2 Are there consistent site-level and landscape-scale factors associated with regeneration?

We used a multi-staged modelling process to explore the site-level and landscape-scale variables associated with the presence of eucalypt regeneration. In the initial stages of analysis, we removed highly correlated variables from further analysis, then modelled sets of candidate site-level and landscape-scale variables separately. For each year-by-study combination, we ran all-subsets regressions (Miller, 1990) with up to six predictor variables, assuming a Bernoulli distribution with a logit-link function for the response (regeneration presence). This analysis allowed us to reduce the number of candidate variables included in the final models for each study. We selected the best model from all possible models for each year-by-study combination based on Akaike's Information Criterion (AIC; Akaike, 1973). We present the selected models in Table A.4.

We subsequently fitted a sequence of GLMMs to construct a ‘global’ spatiotemporal model of variables associated with regeneration. For all models, we assumed a Bernoulli distribution with a logit-link function for the response (regeneration presence).

The construction of our global model involved two stages. First, we fitted GLMMs for each study, including as fixed effects the site-level and landscape-scale predictor variables identified as important across years in the initial all-subsets regressions (Table A.4). For study-level models, we also included Year and Site as random effects (except for Nanangroe where only one year of data were collected). We then fitted a ‘global’ GLMM for the entire study area (i.e. all four study regions combined). Here, we only included as fixed effects site-level and landscape-scale predictors contributing significantly to two or more study-level models (see Table A.5). We also included IBRA subregion as a fixed effect to determine whether regeneration occurrence varied between bioclimatic regions. We included Year and Site nested within Study as random effects. At each stage of modelling, we used Wald tests to assess the significance of each predictor variable included in the model.

We conducted all statistical analyses in GenStat 16 (VSN International Ltd).

3. RESULTS

3.1 Are rates of regeneration declining through time?

We found that rates of eucalypt regeneration were relatively stable through time across the study area, and that the proportion of sites supporting eucalypt regeneration in different IBRA subregions did not vary significantly through time (BBMP: $\chi^2_1 = 1.55$, $P = 0.213$; SWS: $\chi^2_1 = 2.14$, $P = 0.143$; Stewardship: $\chi^2_8 = 5.48$, $P = 0.705$). In the BBMP and SWS study regions, there were slight increases in the proportion of sites supporting regeneration, from 45% in 2010 to 48% in 2012 for BBMP (Fig. 2a) and from 49% in 2008 to 54% in 2013 for SWS (Fig. 2b). There was a slight decrease in the proportion of sites supporting eucalypt regeneration in the Stewardship study from 45% in 2010 to 44% in 2014 (Fig. 2c). However, these patterns were not significant (BBMP: χ_1^2 = 0.10, P = 0.750; SWS: χ_1^2 = 0.25, P = 0.615; Stewardship: χ_2^2 = 0.06, P = 0.969).

3.2 Are there consistent site-level and landscape-scale factors associated with regeneration?

A combination of site-level and landscape-scale variables were associated with eucalypt regeneration. Continuous grazing was negatively associated with the presence of regeneration, while intermittent or no grazing was positively associated with the presence of regeneration (Table 1). Exotic ground cover and natural soil fertility had negative associations with regeneration presence, while elevation and native plant species richness had positive associations with regeneration presence (Table 1). The presence of regeneration was not influenced by IBRA subregion (χ_7^2 = 7.70, P = 0.359).

4. DISCUSSION

Worldwide, evidence suggests that agricultural landscapes are experiencing a native tree regeneration crisis (Fischer et al., 2009). Without sufficient rates of regeneration, these landscapes will gradually lose scattered trees (Dufour-Dror, 2007; Fischer et al., 2010) and their ecosystem services (Manning et al., 2006), potentially leading to broad-scale ecosystem collapse. Hence, to effectively manage agricultural landscapes, it is imperative that we understand what levels of regeneration are occurring across landscapes, and quantify the factors influencing successful regeneration events.

In this paper, we sought to determine and quantify: (1) whether rates of natural regeneration are declining through time in agricultural landscapes, and (2) whether there are consistent site-level and landscape-scale factors associated with natural regeneration across broad spatiotemporal scales. We found that between 2008 and 2014, the proportion of sites supporting eucalypt regeneration in the three study regions analysed (BBMP, SWS and Stewardship) was stable, but low (between 44% and 54%) compared with reported baseline rates of regeneration in unmodified woodlands (91 – 100%; Gibbons et al., 2008a). During 2008 to 2014, we also found variables consistently associated with the occurrence of regeneration across broad spatial scales (i.e. across an area of ~300 000 km^2). Regeneration was more likely to occur on sites: (1) at higher elevations, (2) with higher levels of native plant species richness, (3) where the ground layer was not dominated by exotic plants, (4) where natural soil fertility was lower, and (5) where continuous grazing was not practiced.

4.1 Are rates of natural regeneration declining?

Despite relatively stable patterns in regeneration rates for the duration of this study, the rates are up to 56% (range: 37% to 56%) lower than baseline measurements in undisturbed woodlands (Gibbons et al., 2008a), and these low rates of regeneration are much more widespread than previously established (see Dorrough and Moxham, 2005; Fischer et al., 2009; Weinberg et al., 2011). While the patterns we observed in this study do not cover a period long enough to necessarily be indicative of long-term regeneration trends given the longevity of eucalypts (Noble, 1984), the widespread lack of natural regeneration even over intermediate time-frames is still concerning. If low regeneration rates eventually translate to a loss of tree cover, then there will be major consequences for ecosystem services in future (e.g. connectivity and adaptation to climate change; Manning et al., 2006). Thus, we cannot continue with a ‘business-as-usual’ approach to land management in agricultural areas if we are to prevent the loss of scattered trees from these landscapes. As other researchers have argued (see Kabii and Horwitz, 2006; Morris et al., 2000), we must encourage the uptake of conservation initiatives by landholders through mechanisms like incentive payments. We also must look, in future, to scale up current farm-by-farm initiatives to landscape-scale strategies – such as collaborative agri-environment schemes (McKenzie et al., 2013) – to facilitate ecoregion-wide management of scattered trees and enhanced regeneration success in production landscapes.

4.2 Agricultural intensification and the fate of eucalypts

In several regions of the world (Matson et al., 1997; Tilman et al., 2011), including Australia (DAFF, 2013), the current trend is to intensify agricultural practices. Therefore, strategic implementation of conservation initiatives to promote natural regeneration in agricultural landscapes is essential. Agricultural intensification (e.g. increased stocking rates, fertilizer and/or exotic forage plant addition, and crop sowing) is a highly transformative process that will inhibit natural regeneration (Dorrough and Moxham, 2005; Weinberg et al., 2011). Intensifying agricultural production often involves, among other strategies, increasing soil fertility through nutrient addition, which reduces the likelihood of successful eucalypt regeneration in Australia (Fischer et al., 2009; Skinner et al., 2010). Soil nutrient enrichment is also associated with the introduction of, or invasion by, exotic plants (Dorrough and Moxham, 2005; McIntyre, 2008) that can reduce the competitive ability and persistence of many native plant species, including young eucalypts (Dorrough et al., 2006; Dorrough and Scroggie, 2008; McIntyre, 2012). Hence, without careful management of farmlands, there will be a loss of eucalypts across large areas of agricultural Australia through low rates of natural regeneration.

Two potential management strategies for balancing eucalypt conservation with agricultural production are land sparing and land sharing (or wildlife-friendly farming) (Green et al., 2005). These strategies have been discussed extensively (see reviews by Fischer et al., 2014; Norris, 2008) and there is support for use of both land sparing (Egan and

Mortensen, 2012; Hulme et al., 2013) and land sharing (Nájera and Simonetti, 2010; Pywell et al., 2012). However, in landscapes where there is considerable overlap between the distribution of threatened ecoregions and lands preferentially used for agriculture (as is the case in our study region; Rayner et al., 2014), there is an increasing recognition that a **combination** of land sharing and land sparing is needed across broad spatial scales to best meet production and biodiversity conservation needs (see Fischer et al., 2008; Grau et al., 2013).

Designing and implementing a broad-scale agri-environment scheme like the Environmental Stewardship Program in Australia is a complex task. As a first step, we argue that systematic targeting of farms more suited to land sharing or land sparing will facilitate the creation of a landscape-scale patchwork of land-sharing and land-sparing strategies that can effectively conserve eucalypts in agricultural landscapes. Our results show that the occurrence of natural regeneration is negatively associated with explanatory variables coincident with agricultural intensification. These variables include continuous livestock grazing, increased exotic plant cover (encouraged by the use of fertilisers; McIntyre, 2012), increased natural soil fertility (as, historically, areas with more fertile soils were preferentially modified and improved for agricultural purposes; Yates and Hobbs, 1997), and decreased elevation (as agriculture was preferentially established and intensified in low lying areas; Yates and Hobbs, 1997). This suggests that the sustainable management of natural ecosystems is not consistent with agricultural intensification (i.e. areas with high stocking rates, fertilizer and/or exotic forage plant addition, or crop sowing). Hence, we recommend that a land-sharing strategy should be prioritised, and incentive payments allocated to offset production opportunity costs (see House et al., 2008), in locations where: (1) the land can be managed with intermittent or no grazing, (2) the ground layer is not dominated by exotic plants, and (3) natural soil fertility is low. Natural regeneration is most likely to occur under such conditions, provided there has been limited or no fertiliser use on the land as elevated phosphorus levels suppress eucalypt regeneration (see Fischer et al., 2009; Wilkins et al., 2003). Here, incentive payments to encourage uptake of conservation initiatives are more likely to yield successful conservation outcomes regarding regeneration, inducing decision makers to outlay the often considerable costs associated with agri-environment incentive schemes (see Batáry et al., 2015; Berendse et al., 2004).

Conversely, for continuously grazed and exotic-dominated locations, a land-sparing strategy (where production can be intensified for the most part, provided that relatively intact remnants are reserved elsewhere) is likely to be more appropriate. Here, it may be best to manage farmland to maximise production because the land is likely to have been altered to the point that it can no longer support natural eucalypt regeneration (Hobbs, 2010; McIntyre, 2012). In these areas, remnant tree cover (including scattered paddock trees) should still be retained and protected, and their standing life maximised where possible. However, the next generation of trees in agricultural landscapes would best be established in areas where the process of natural regeneration can be supported. That is, in response to increasing demand for global food production, we should begin to "move" tree cover and actively encourage natural tree regeneration in agricultural landscapes from places where it is less likely to be managed sustainably, to places where it can be. Initially, a land sparing strategy may manifest as patches of trees around, or near to, the individual farms on which the scattered paddock trees are being lost. In future, under collaborative agri-environment schemes, land sparing may see groups of high-production farms collectively reserving large tracts of adjacent lands – within the same bioregion – for conservation (see Balmford et al., 2012 for a schematic diagram). The long-term co-existence of production and regeneration in intensively managed lands may be possible where direct seeding or planting and fencing of remnants is employed. This may complement strategies to maximise natural regeneration at the landscape scale, but such actions are costly in terms of time and money (Dorrough and Moxham, 2005) potentially influencing long-term participation in agri-environment schemes by landholders (Dobbs and Pretty, 2008; McKenzie et al., 2013).

While these recommendations would facilitate biodiversity conservation in agricultural landscapes, decision making requires further considerations. Prioritising conservation actions (or alternatively intensification of production) cannot solely rely on resource allocation informed by spatial correlates of natural tree regeneration. Options for land sparing and land sharing are also constrained by historical and contemporary land use (Duncan and Dorrough, 2009), the ecology of the locale and region (Fischer et al., 2008), and social and economic imperative (i.e. landholders ultimately control farm management and often look to offset opportunity costs incurred by undertaking conservation actions; Pascual and Perrings, 2007). To adequately assess current *trends* in eucalypt regeneration under such constraints, and to tease apart effects of historical versus contemporary land use on broad-scale regeneration occurrence, longer-term analyses are required (> 10 years) to complement and extend studies such as the one we present here.

5. CONCLUSIONS

Securing the persistence of natural regeneration and scattered trees in agricultural landscapes is a complex problem that requires a strategic and multi-scaled approach to balance the apparently conflicting demands of increased agricultural production with the conservation and maintenance of native vegetation cover. We suggest that to improve natural eucalypt regeneration while meeting agricultural production demands, it will be important to differentiate between landscapes more suited to agricultural intensification/land sparing and those that are likely to benefit from land sharing, based on the prevalence of natural regeneration. To maximise the effectiveness, and success, of conservation initiatives designed to promote natural regeneration throughout agricultural landscapes, ongoing monitoring is needed to capture temporal and spatial variations in the patterns of natural regeneration as well as the environmental variables influencing those patterns.

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Supplementary data associated with this article can be found, in the online version, at XXX.

TABLES

Table 1. Coefficients for site-level and landscape-scale variables associated with eucalypt regeneration across four study regions in south-eastern Australia. The significance levels are from tests of the effect of the variable across all studies.

	Estimate	SE	Wald	df	*P*
Coefficients for grazing intensity			34.32	2	< 0.001
Continuous	-0.665	0.516			
Intermittent	0.611	0.502			
Absent	0.767	0.509			
Native plant species richness	0.068	0.016	19.19	1	< 0.001
% Exotic ground cover	-0.011	0.003	12.47	1	<0.001
Elevation (m)	0.003	0.001	17.27	1	<0.001
Natural soil fertility	-0.226	0.061	13.60	1	<0.001

FIGURE CAPTIONS

Figure 1. Map of the four study regions. (a) Extent of study regions in south-eastern Australia. (b) Location of individual sites, represented by open circles, in New South Wales (NSW), along the eastern border of the Australian Capital Territory (ACT) and in southern Queensland (QLD). Shading indicates separate study regions: dark grey = Biodiversity Baseline Monitoring Program (BBMP), white = South-west slopes (SWS), black = Nanangroe, pale grey = Environmental Stewardship Program (Stewardship).

Figure 2. Predicted mean proportion of sites (± 95% CI) with regeneration present through time, in three study regions: (a) BBMP, (b) SWS, and (c) Stewardship.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix A. Detailed descriptions of the study regions included in analyses.

Table A.1. Definitions and collections methods for site-level variables used in analyses.

Table A.2. Definitions and collections methods for landscape-scale and weather variables used in analyses.

Table A.3. Details of years of data collection included in each analysis.

Table A.4. Variables included in generalised linear models (GLMs) for each year-by-study combination.

Table A.5. Variables included in generalised linear mixed models (GLMMs) for four study regions and a final, global model.

Appendix A. Detailed descriptions of the four study regions (Murray Biodiversity Baseline Monitoring Program, South-west Slopes, Nanangroe and Environmental Stewardship Program) included in analyses.

Murray Biodiversity Baseline Monitoring Program

The Murray Biodiversity Baseline Monitoring Program ('BBMP') is the southernmost study region. Sites are stratified by four vegetation communities: floodplain transition woodland dominated by grey box (*Eucalyptus microcarpa*), inland floodplain woodland dominated by black box (*E. largiflorens*), riverine plain woodland dominated by boree (*Acacia pendula*) and riverine sandhill woodland dominated by white cypress pine (*Callitris glaucophylla*) and yellow box (*E. melliodora*) (see Keith, 2004); and four land management classes: production sites where woodland is used for agricultural purposes including livestock grazing and cropping, short-term conversion sites where woodland has been protected under a management agreement since 2007, long-term conversion sites where woodland has been managed for biodiversity outcomes since 2003, and travelling stock reserves where woodland is infrequently grazed and has not been subject to extensive vegetation clearing (Lentini et al., 2011). For more details see Lindenmayer et al. (2012) and Michael et al. (2014). We excluded saltbush plantings from analysis for this paper.

South-west slopes restoration study

The South-west slopes restoration study ('SWS') overlaps with the BBMP study region but encompasses different vegetation communities (including western slopes grassy woodlands, upper riverina dry sclerophyll forests and inland riverine forests) dominated by white box (*E. albens*), grey box, yellow box, Blakely's red gum (*E. blakelyi*), red stringybark (*E. macrorhyncha*) and red ironbark (*E. sideroxylon*). Similar to BBMP, land-use history is dominated by domestic livestock grazing and cropping. In this study region, sites are stratified by two farm types: with native vegetation plantings and without native vegetation plantings, and four vegetation forms: native revegetation plantings established to mitigate soil erosion and salinity problems, coppice regrowth from existing trees recovering from fire or logging or both, seedling regrowth establishing from native overstorey seed fall and old-growth woodland dominated by large, old trees. For more details see Cunningham et al. (2007). We excluded plantings from analysis for this paper.

Nanangroe study

The Nanangroe study lies approximately 100 km to the east of the SWS study region. Post-European settlement the area was extensively cleared, primarily for domestic livestock grazing. Patches of remnant vegetation remain varying in size from < 1 ha to approximately 15 ha and are dominated by yellow box, red box (*E. polyanthemos*), white box, Blakey's red gum and red stringybark. Sites in this study were assigned to one of four landscape context classes: woodland remnants surrounded by radiata pine plantations, stands of radiata pine, woodland remnants located on semi-cleared land primarily used for livestock grazing, and cleared grazing paddocks. For further details see Lindenmayer et al. (2001). We excluded remnants surrounded by pine plantations and cleared grazing paddocks from analysis for this paper.

Environmental Stewardship Program

The Environmental Stewardship Program ('Stewardship') covers the greatest area of all study regions (172 232 km2; Lindenmayer et al., 2012). As part of an Australian Government environmental initiative, farms were strictly selected to conserve threatened box gum grassy woodland (Lindenmayer et al., 2012) with an overstorey dominated or co-dominated by yellow box, white box, Blakely's red gum or grey box (TSSC, 2015). For the study, paired sites were established on each farm. One site was located in the funded woodland patch. The second site acted as a control and was exposed to usual farm management practices such as grazing, and invasive plant and animal control (Lindenmayer et al., 2012). In southern New South Wales, additional sites were established on 29 farms as part of a grazing study to compare how four different grazing management practices influence ecosystem properties, including short holistic grazing, long holistic grazing, continuous grazing and grazing exclusion.

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Table A.1. Definitions and collections methods for site-level variables used in analyses. Variables were compared across sites in four study regions to investigate associations with natural eucalypt regeneration through time.

Attribute	Data description	Scale	Data type (period)	DEM resolution	Software
Native ground cover (grasses)	% cover of native grass species, calculated as a % of presences from observations at 100 points along two 50 m transects	Site	Temporal (2008-2014)	-	-
Native ground cover (shrub)	% cover of native woody species < 1 m in height, calculated as a % of presences from observations at 100 points along two 50 m transects	Site	Temporal (2008-2014)	-	-
Native ground cover (other)	% cover of native vascular plant species other than grasses or shrubs < 1 m in height, calculated as a % of presences from observations at 100 points along two 50 m transects	Site	Temporal (2008-2014)	-	-
Exotic ground cover	% cover of all exotic plant species, calculated as a % of presences from observations at 100 points along two 50 m transects	Site	Temporal (2008-2014)	-	-
Bare ground	% cover of bare ground, calculated as a % of presences from observations at 100 points along two 50 m transects	Site	Temporal (2008-2014)	-	-
Rock cover	% cover of rocks > 5 cm, calculated as a % of presences from observations at 100 points along two 50 m transects	Site	Temporal (2008-2014)	-	-
Leaf litter cover	% cover of leaf litter, calculated as a % of presences from observations at 100 points along two 50 m transects	Site	Temporal (2008-2014)	-	-
Soil crust cover	% cover of soil crusts, calculated as a % of presences from observations at 100 points along two 50 m transects	Site	Temporal (2008-2014)	-	-
Native overstorey cover	Visual estimate of % cover for native canopy and sub-canopy tree species > 4 m tall using images in Walker and Hopkins (1990), averaged over 20 points along two 50 m transects	Site	Temporal (20108-2014)	-	-
Native mid-storey cover	Visual estimate of % cover for native plant species (including regenerating tree species) that are 1-4 m tall using images in Walker and Hopkins (1990), averaged over 20 points along two 50 m transects	Site	Temporal (2008-2014)	-	-
Native plant species richness	Number of native plant species in a 20 m x 20 m plot	Site	Temporal (2008-2014)	-	-
Length of fallen logs	Total length (m) of fallen logs with a diameter ≥ 10 cm, averaged over two 50 m x 20 m plots	Site	Temporal (2008-2014)	-	-
Eucalypt regeneration	Measure of eucalypt regeneration (abundance of seedlings/proportion of overstorey species present as regeneration) recorded in two 50 m x 20 m plots	Site	Temporal (2008-2014)	-	-
Keith Class	Class assigned to site using dominant canopy species and main associated species according to Keith (2004) and with reference to *BioMetric* Vegetation Type spreadsheet (OEH, 2014).	Site	Temporal (2008-2014)	-	-
Grazing intensity	Categorical assignment of approximate grazing intensity based on the frequency of grazing across a three-year period (2005-2008 for BBMP & SWS, 2007-2010 for Stewardship & Nanangroe). The three categories we used were: no grazing (< 7 days of lightly stocked grazing per year), intermittent grazing (≤ 6 months grazing per year with varying levels of stocking), and continuous grazing (> 6 months grazing per year with varying levels of stocking).	Site	Static	-	-
Native woody cover (250 m)	Landsat satellite imagery is used to discriminate between forest and non-forest cover. Forest cover (here named “native woody cover”) is defined as vegetation with a minimum 20% canopy cover, > 2 m high and a minimum area of 0.2 ha. NB: this product does not adequately represent sparse open woodland or scattered trees. Using ArcGIS, we calculated the mean proportion of woody cover in a 250 m buffer around each site.	250 m buffer around site	Static		ArcGIS

References (for Table A.1)

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Table A.2. Definitions and collection methods for landscape-scale and weather variables used in analyses. Variables were compared across sites in four study regions to investigate associations with eucalypt regeneration through time.

Attribute	Data description	Scale	Data type (period)	Resolution	Software
Landscape variables					
Elevation	Elevation of each site estimated from 1:100 000 topographic map contours.	Point measure for site	Static		ArcGIS
Aspect (northern/eastern)	Northern and eastern components of aspect were calculated along north-south and east-west axes respectively at each grid cell of the national 9 sec DEM. These are recorded as continuous values between 1 and -1 where "1" represents due north (north-south axis) or due east (east-west axis), and "-1" represents due south (north-south axis) or due west (east-west axis).	Point measure for site	Static mean	9 sec	ArcGIS
Topographic wetness index (TWI)	Mean topographic wetness index (TWI) is derived by dividing contributing catchment by slope at each grid cell of the national 9 sec DEM. It is a continuous terrain-based measure of position in the landscape, ranging from negative values on ridges (with no contributing catchment) and upper slopes (small contributing catchment/steep slope) to increasingly higher positive values through lower slopes, valley flats and eventually drainage lines.	Mean TWI for 250 m buffer around site	Static mean	9 sec	ArcGIS
Accumulated runoff	Accumulated runoff is a measure of soil water surplus from GROWEST water balance calculations at each grid cell of the national 9 sec DEM, using rainfall and evaporation surfaces are used in conjunction with soil texture and water-holding characteristics. Derived values are summed through the landscape according to flow-accumulation analyses to provide a single value for accumulated runoff. This value is a continuous measure ranging from low, positive values (drier upslope land) to high, positive values for wetter areas and/or areas lower in the catchment.	Mean runoff for 250 m buffer around site	Static mean	9 sec	ArcGIS
Natural soil fertility	The mean natural soil fertility is a simple ordinal index (2-12) of substrate fertility based on underlying lithology. The index assumes, all other things being equal, that bedrocks with a low rank (2-5) yield low fertility soils for plant growth and rocks with a high rank yield high fertility soils for plant growth (6-10). Bedrock with extremely high rank (11-12) yields potentially toxic soils for plant growth. See deVries (2009).	Point measure for site	Static mean	36 sec	ArcGIS
IBRA region & subregion	Classification of Australia's landscapes into 89 large geographically distinct bioregions based on common climate, geology, landform, native vegetation and species information (IBRA region). IBRA bioregions are further divided into 419 subregions based on localised and homogenous geomorphologies (see Australian Government, 2013).	Point classification for site	Static	9 sec	ArcGIS
Weather variables					
Two-year mean annual maximum temperature	Site estimates derived from elevation dependent interpolations of weather station data using thin plate smoothing splines	Point measure for site	Annual mean for 2-year period (year of survey and year preceding survey)		ANUClim
Two-year mean annual rainfall	Site estimates derived from elevation dependent interpolations of weather station data using thin plate smoothing splines	Point measure for site	Annual mean for 2-year period (year of survey and year preceding survey)		ANUClim
Mean seasonal rainfall (winter, spring, summer)	Site estimates derived from elevation dependent interpolations of weather station data using thin plate smoothing splines	Point measure for site	Seasonal mean (June-Aug, Sept-Nov, Dec-Feb) for 2-year period (year of survey and year preceding survey)		ANUClim
Plant growth index	Site estimates derived from GROWEST (Hutchinson et al., 2004; Nix, 1981) by combining soil moisture index (calculated from a water balance model using monthly rainfall and pan evaporation) with temperature and solar radiation indices to summarise weather conducive to plant growth	Point measure for site	Static mean		ANUClim

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Table A.3. Details of years of data collection included in each analysis (trends in rates of eucalypt regeneration through time, and environmental determinants of eucalypt occurrence) for four study regions (BBMP, Nanangroe, SWS, Stewardship).

Analysis/Study	Years included
Trends analysis	
BBMP	2010, 2012
SWS	2008, 2013
Stewardship	2010/2011, 2012, 2014
Environmental determinants analysis	
BBMP	2010, 2012
Nanangroe	2010
SWS	2008, 2013
Stewardship	2010/2011, 2014

Table A.4. Variables included in generalised linear models (GLMs) for each year-by-study combination, based on AIC-selected best subsets linear models with six predictor variables. Details are provided for all models with AIC or SIC < 2. The four study regions are Biodiversity Baseline Monitoring Program (BBMP), South-west slopes (SWS), Nanangroe and Environmental Stewardship Program (Stewardship). The site-level candidate variables we used in the GLMs included: grazing intensity (**grazing**) , % bare ground cover (**bare**), % soil crust cover (**crust**), % exotic ground cover (**EGC**), % litter cover (**LLC**), % mid-storey cover (**MSC**), % native grass cover (**NGC**), % native shrub cover < 1 m in height (**NSC**), % other native cover (e.g. ferns) (**NOC**), % overstorey cover (**OSC**), % rock cover (**rock**), total length of fallen logs > 10 cm diameter (**logs**), total native plant species richness (**NPS_rich**), Keith vegetation community class (**keith_class**), proportion of native woody cover in a 250 m buffer around the site (**woody250**). The landscape-scale candidate variables we used included: latitude (**lat**), elevation (**elev**), northerly aspect (**aspN**), easterly aspect (**aspE**), long-term mean annual plant growth index adjusted for soil type (**AMGrowth**), natural soil fertility (**soil_fert**), mean topographic wetness index in a 250 m buffer around the site (**TWI**), mean accumulated runoff in a 250 m buffer around the site (**accRO**), two-year mean annual maximum temperature (**AnnMaxTemp**), two-year mean autumn precipitation (**AutP**), two-year mean spring precipitation (**SprP**), two-year mean summer precipitation (**SumP**). Selected models are indicated by bold text.

Region	Scale	Year	Included Variables	AIC
BBMP	Site	2010	**grazing + NGC + NOC + woody250**	**88.08**
			grazing + NGC + woody250	89.87
	Landscape	2010	**soil_fert**	**112.17**
	Site	2012	**NPS_rich**	**109.61**
	Landscape	2012	**AMGrowth + soil_fert + SumP**	**97.34**
			lat + soil_fert + AnnMaxT + SumP	98.27
Nanangroe	Site	2010	**EGC + keith_class + woody250**	**99.78**
			grazing + EGC	101.82
	Landscape	2010	**elev + soil_fert + AnnMaxT + SprP + TWI**	**81.96**
			elev + soil_fert + lat + AnnMaxT + TWI	83.78
			elev + soil_fert + AnnMaxT + SprP	85.77
SWS	Site	2008	**grazing + MSC + NGC + OSC**	**72.27**
	Landscape	2008	**no variables significant**	**-**
	Site	2013	**grazing + bare + EGC + logs + NGC + NSC**	**81.44**
			bare + EGC + logs + NGC + NSC	84.06
			grazing + logs + NSC	86.95
	Landscape	2013	**elev**	**99.44**
			SprP	100.58
			AnnMaxT	100.83
Stewardship	Site	2010/2011	**grazing + EGC + LLC + NOC + NPS_rich + OSC**	**220.52**
			grazing + EGC + LLC+ NOC + NPS_rich + woody250	221.96
	Landscape	2010/2011	**elev**	**264.80**
	Site	2014	**grazing + keith_class + NPS_rich**	**228.93**
	Landscape	2014	**elev + soil_fert**	**239.37**
			elev	242.24

Table A.5. Variables included in generalised linear mixed models (GLMMs) for four study regions: Baseline Biodiversity Monitoring Scheme (BBMP), South-west slopes (SWS), Nanangroe, Environmental Stewardship Program (Stewardship); and variables included in the ‘global’ GLMM. See Table A.4 caption for variable acronyms.

Region	**Model Fitted**	**Estimate**	**SE**	***Wald***	**df**	***P***
BBMP	*FIXED:* grazing + NGC + woody250 + NPS_rich + AMGrowth + soil_fert + SumP					
	RANDOM: Site + Year					
	Significant variables:					
	grazing			12.48	2	0.002
	continuous grazing	-1.358	0.405			
	intermittent grazing	0.671	0.416			
	no grazing	0.081	0.287			
	NPS_rich	0.136	0.046	8.81	1	0.003
	NGC	0.027	0.010	6.75	1	0.009
	soil_fert	-0.580	0.149	15.07	1	<0.001
Nanangroe	*FIXED:* EGC + keith_class + woody250 + elev + soil_fert + AnnMaxT + SprP + TWI					
	RANDOM: Site					
	Significant variables:					
	EGC	-0.042	0.017	6.00	1	0.014
	elev	0.410	0.145	8.02	1	0.005
	soil_fert	-0.638	0.285	5.01	1	0.025
	AnnMaxtT	76.420	25.177	9.21	1	0.002
	SprP	0.998	0.276	13.02	1	<0.001
SWS	*FIXED:* grazing + bare + EGC + logs + MSC + NGC + NSC + OSC + elev					
	RANDOM: Site + Year					
	Significant variables:					
	logs	-0.012	0.005	5.18	1	0.023
Stewardship	*FIXED:* grazing + EGC + keith_class + LLC + NOC + NPS_rich + OSC + elev + soil_fert					
	RANDOM: Site + Year					
	Significant variables:					
	grazing			12.77	2	0.002
	continuous grazing	-1.356	0.395			
	intermittent grazing	-0.199	0.157			
	no grazing	0.444	0.312			
	NPS_rich	0.098	0.022	20.15	1	<0.001
	NOC	-0.026	0.012	4.48	1	0.034
	EGC	-0.013	0.004	8.34	1	0.004
	elev	0.003	0.001	12.95	1	<0.001
GLOBAL	*FIXED:* IBRA subregion + grazing + EGC + NPS_rich + elev + soil_fert					
	RANDOM: Study/Site + Year					
	Significant variables:					
	grazing			34.32	2	<0.001
	continuous grazing	-0.665	0.516			
	intermittent grazing	0.611	0.502			
	no grazing	0.767	0.509			
	NPS_rich	0.068	0.016	19.19	1	<0.001
	EGC	-0.011	0.003	12.47	1	<0.001
	elev	0.003	0.001	17.27	1	<0.001
	soil_fert	-0.226	0.061	13.60	1	<0.001

FIGURES

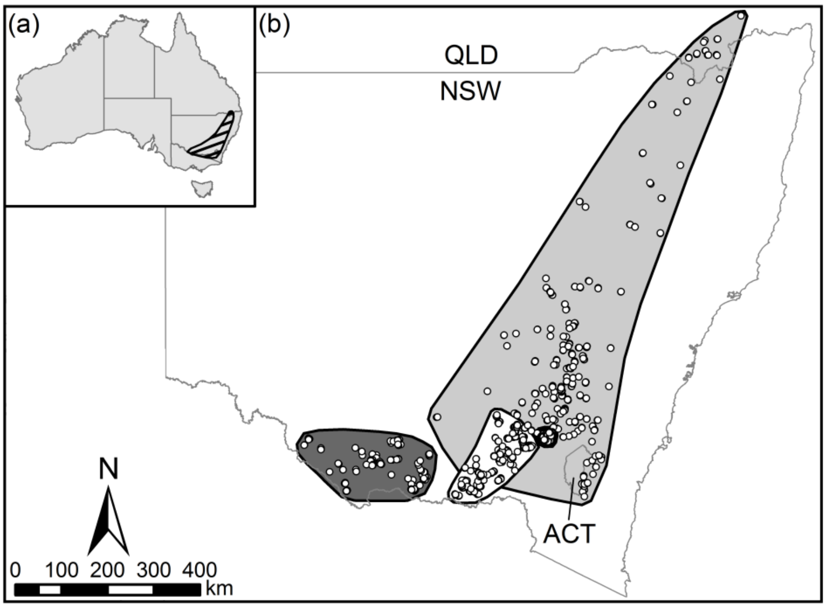

Figure 1.

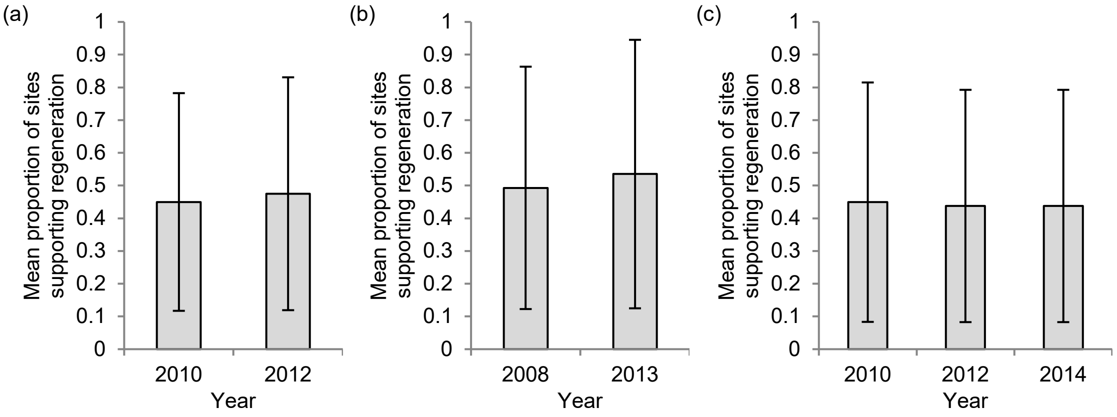

Figure 2.