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RESEARCH ARTICLE

Restoration promotes recovery of woodland birds in agricultural environments: A comparison of 'revegetation' and 'remnant' landscapes

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Abstract

1. Ecological restoration in rural environments is a global challenge for the 21st century. Restoration measures—such as agri-environment activities, woodlots, natural regeneration and conservation plantings—collectively alter landscape structure with the aim of restoring conservation values that are characteristic of natural ecosystems. We tested the landscape-scale benefits of restoration for woodland birds, species of conservation concern in southern Australia, by assessing the richness and composition of avian communities in rural landscapes along a gradient in habitat restoration, benchmarked against landscapes with comparable extent of native vegetation.
2. We selected 43 landscapes (each 8 km^2) in Victoria, Australia, representing: (a) a trajectory of decline in the extent of remnant native wooded vegetation ('remnant' landscapes), (b) a trajectory of gain in planted vegetation ('revegetation' landscapes) and (c) a similar gradient comprising a mix of remnants and planted vegetation ('mixed' landscapes). In each landscape, repeat surveys of birds were undertaken at 12 sites, stratified in relation to land cover.
3. Species richness of all terrestrial and woodland birds showed similar positive responses to total wooded cover in each landscape type, but woodland birds had reduced richness in 'revegetation' relative to 'remnant' and 'mixed' landscapes. Across all landscapes, key factors influencing richness were the extent of wooded cover and proportion comprised of plantings, scattered trees in farmland and mean annual rainfall. The composition of woodland bird assemblages differed between 'remnant' and 'revegetation' landscapes with predictable differences associated with foraging traits.
4. *Synthesis and applications*. Restoration plantings stimulate recolonisation of otherwise-depleted landscapes, effectively reversing a decline in woodland birds. Key insights include: (a) benchmarking 'revegetation' against 'remnant' landscapes provides a valuable means to quantify restoration outcomes at the

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landscape scale; (b) time-lags in vegetation maturation contribute to a trajectory of recovery that differs from a trajectory of decline, in both richness and composition of the avifauna; (c) scattered trees have a critical role for avifaunal conservation in farm landscapes; (d) restoration plantings are most effective in 'mixed' landscapes, where complementary resources from remnant and planted vegetation are juxtaposed; and (e) restoration plantings on individual farms contribute to landscape-scale biodiversity gains while also having socio-ecological and production benefits.

KEYWORDS
Australia, farmland birds, landscape planning, plantings, reforestation, restoration trajectory, revegetation, woodlot

1 | INTRODUCTION

Ecosystem restoration is firmly on the global agenda (Aronsen & Alexander, 2013). Recent initiatives such as the United Nations Decade of Restoration (Fischer et al., 2021) have set ambitious targets for restoring millions of hectares world-wide. Such restoration is most urgently needed in agricultural regions where land transformation to produce food and fibre has had profound environmental impacts. Restoration in these regions will necessarily occur in, and among, productive 'working' landscapes (Kremen & Merenlender, 2018), through a variety of measures such as agroforestry plantings, shelterbelts, natural regeneration, agri-environment programs, rewilding and conservation plantings (Munro et al., 2007; Murgueitio et al., 2011; Batáry et al., 2015). These measures alter the composition and structure of rural landscapes.

For fauna, restoration typically aims to counter the detrimental effects of habitat loss, fragmentation and degradation (Vickery & Arlettaz, 2012; McAlpine et al., 2016) by expanding the overall extent of suitable habitat, increasing habitat heterogeneity, adding elements to enhance connectivity, providing resources for specialist species and improving the quality of degraded habitats (Thomson et al., 2009; Kremen & Merenlender, 2018). Such landscape change is hypothesised to benefit biodiversity by increasing populations of extant species, rescuing declining populations and preventing local extinctions, attracting species 'back' into the landscape through recolonisation and enhancing ecosystem function through restoring interspecific interactions (e.g. pollination and seed dispersal; Munro et al., 2007; Kormann et al., 2016; McAlpine et al., 2016). Socio-ecological benefits from landscape restoration are also important goals, including more sustainable food and timber production and improved human health and well-being (Fischer et al., 2021).

Numerous studies have provided insights into factors that influence the quality of restored habitats at the site or patch scale (e.g. Lindenmayer et al., 2010; Whytock et al., 2018). However, there is growing appreciation of the need to understand conservation requirements at the landscape scale, comprising the heterogenous mosaic of land uses typical of agricultural environments (Harvey et al., 2008; Fahrig et al., 2011). For many species, persistence depends on multiple populations that can interact (i.e. a metapopulation); or the capacity for individuals to obtain resources from multiple patches. Pragmatically, a landscape perspective is relevant to the scale at which land managers set restoration goals and manage for conservation. To test whether restoration achieves landscape-scale benefits, it is necessary to compare 'whole landscapes' (McGarigal & Cushman, 2002) that differ in the extent or pattern of restoration undertaken. Further, given the goal of restoration is to restore biota associated with natural ecosystems, comparing restored landscapes with those containing a similar extent of natural vegetation will allow insight into whether restoration can effectively reverse the process of biodiversity loss at landscape scales.

In Australia, temperate woodlands are among the most highly modified ecosystems with vast areas transformed for agricultural production (Hobbs & Yates, 2000). Excessive loss of vegetation and associated changes to soils, water quality, agricultural production and conservation values have stimulated national programs to restore indigenous vegetation, primarily through planting (revegetation) trees and shrubs (Campbell, 1994; Hajkowicz, 2009). Woodland birds have experienced marked declines and are of national conservation concern (Ford, 2011). Factors influencing their conservation status include extensive loss, fragmentation and degradation of woodlands and altered biotic interactions associated with such landscape change (Radford & Bennett, 2007; Ford, 2011; Mac Nally et al., 2012). Woodland birds frequently are a focus of restoration plans, to enhance their conservation status and because they serve as flagship species to engage landholders and local communities.

We used a landscape-scale, mensurative experiment to assess the benefits of restoration for woodland birds, undertaken through revegetation plantings in a rural region. We systematically surveyed the avifauna in three types of landscape, those in which wooded cover is dominated by: (a) remnant native vegetation ('remnant' landscapes), (b) revegetation plantings ('revegetation' landscapes) and (c) a mix of remnants and plantings ('mixed' landscapes). Replicates of each landscape type spanned a gradient in the extent of wooded cover from ~1% to 19% (the maximum extent available for 'revegetation' landscapes). Thus, our study design allowed direct comparison of the response of the bird community to a trajectory of loss of native vegetation (in remnant landscapes) versus a trajectory of restoration of wooded vegetation (in revegetation and mixed landscapes).

We addressed three main questions.

1. Does landscape type influence the relationship between richness of bird species (all terrestrial species and woodland species) and extent of wooded cover? If replanting of wooded vegetation effectively reverses the loss of habitat for bird species, we expect the relationship between species richness and extent of wooded cover to be similar for each landscape type. Alternatively, if replanting stimulates a different pathway of recovery, relationships may differ.
2. What are the key properties of rural landscapes that influence the richness of woodland birds? We sought to identify the properties of rural landscapes that consistently influence the richness of woodland bird species, including variables representing extent and spatial configuration of wooded vegetation, landscape composition, proximity to potential source areas and climatic variation (rainfall).
3. Does the composition of the woodland bird community in 'revegetation' landscapes match that of 'remnant' landscapes? If restoration results in re-assembly of communities similar to those in remnant landscapes, we expect a similar avifaunal composition in each landscape type. Alternatively, if replanting does not provide the same habitat resources as remnant vegetation, we expect compositional differences to be evident.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is an agricultural region of ~1.5 million ha in temperate, south-western Victoria, Australia (Figure 1). The dominant land use is sheep and cattle grazing on pastures of exotic grasses.

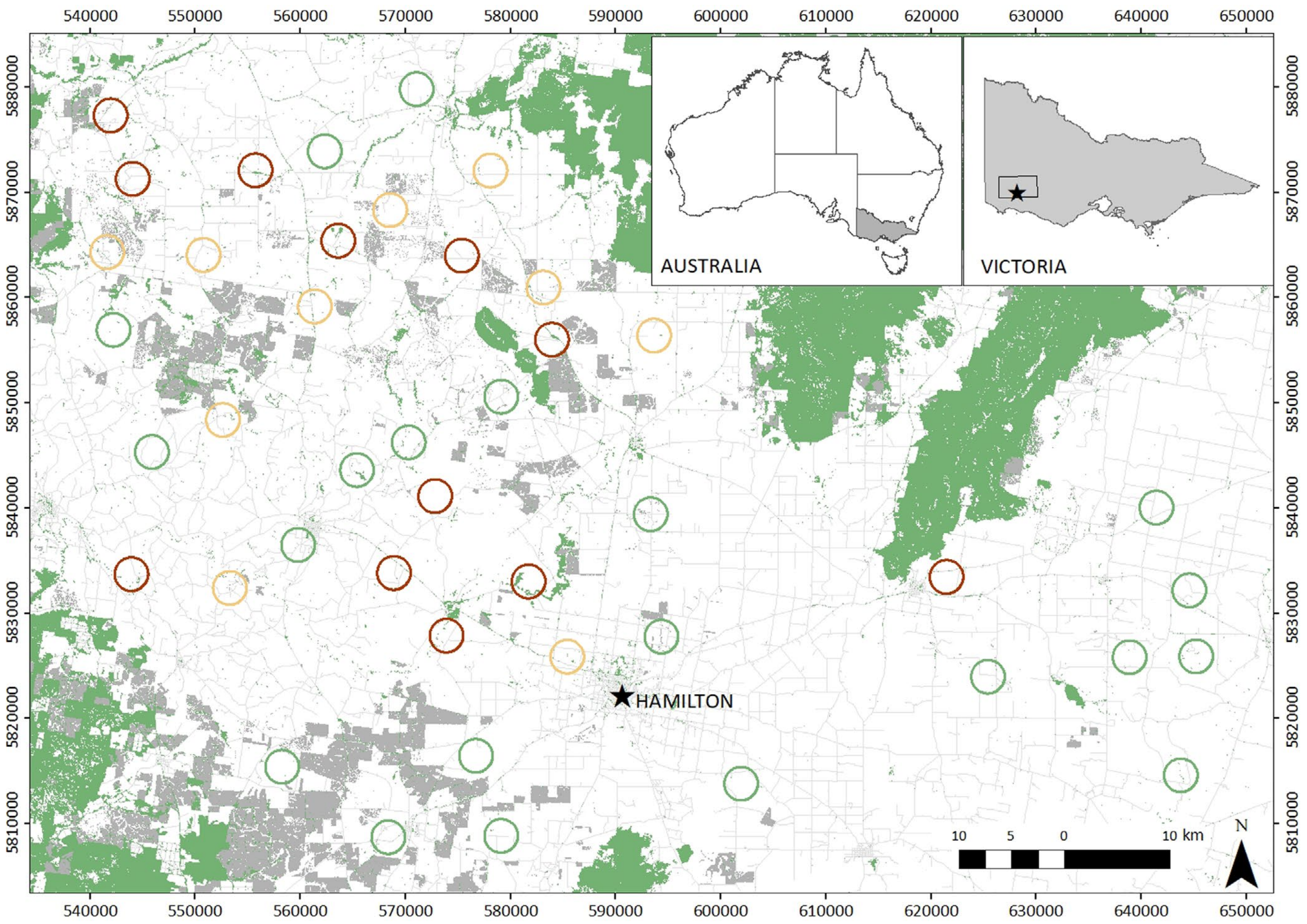

FIGURE 1 Study area in south-western Victoria, Australia, showing the location of 43 study landscapes, each 8 km^2 in size. Colours indicate landscapes classed as 'remnant' (brown), 'revegetation' (green) and 'mixed' (yellow). Large tracts of remnant vegetation (green shading) in the north-east and south-west are in different land systems to the study landscapes. Grey shading represents commercial plantations

Historically, native vegetation comprised grassy open woodlands dominated by *Eucalyptus* species, particularly river red gum *Eucalyptus camaldulensis*, drooping she-oak *Allocasuarina verticillata* and silver banksia *Banksia marginata* over a ground layer of tussock grasses and herbs. Following European settlement (~1840), native vegetation was rapidly cleared (>90%) leaving remnants in conservation reserves, along streams and roadsides, and small patches. In parts of the region, large old trees (*E. camaldulensis*) are scattered extensively across farmland.

Planted vegetation takes two main forms. First, extensive establishment of commercial tree plantations, particularly non-indigenous blue gum (*E. globulus*; Ierodiaconou et al., 2005; Figure 1) has occurred since ~1995. We avoided such areas. Rather, we focussed on landscapes with smaller scale plantings ('revegetation') among farmland, commonly <5 ha in size. These may be for farm productivity (shelterbelts and woodlots), land protection (e.g. reduce erosion along streams) or conservation purposes. Plantings typically have an overstorey of eucalypt tree species with shrubs (e.g. *Acacia* and *Melaleuca*) in the understorey. Such plantings commenced from the 1970s (e.g. Campbell 1991), though some earlier shelterbelts were planted with exotic tree species (*Pinus radiata* and *Cupressus macrocarpa*).

2.2 | Study design

We selected three types of landscapes, with replicates for each representing a gradient in the overall extent of wooded eucalypt cover from <1% to ~19% (see Appendix S1; Figure 2). These were: (a) 'remnant' landscapes (n = 12) in which wooded vegetation was primarily remnant native vegetation (i.e. mean proportion of wooded vegetation comprising remnants = 0.91, range 0.75–0.99); (b) 'revegetation' landscapes (n = 21) dominated by plantings (mean proportion of wooded vegetation comprising plantings = 0.92, range 0.72–1.00);

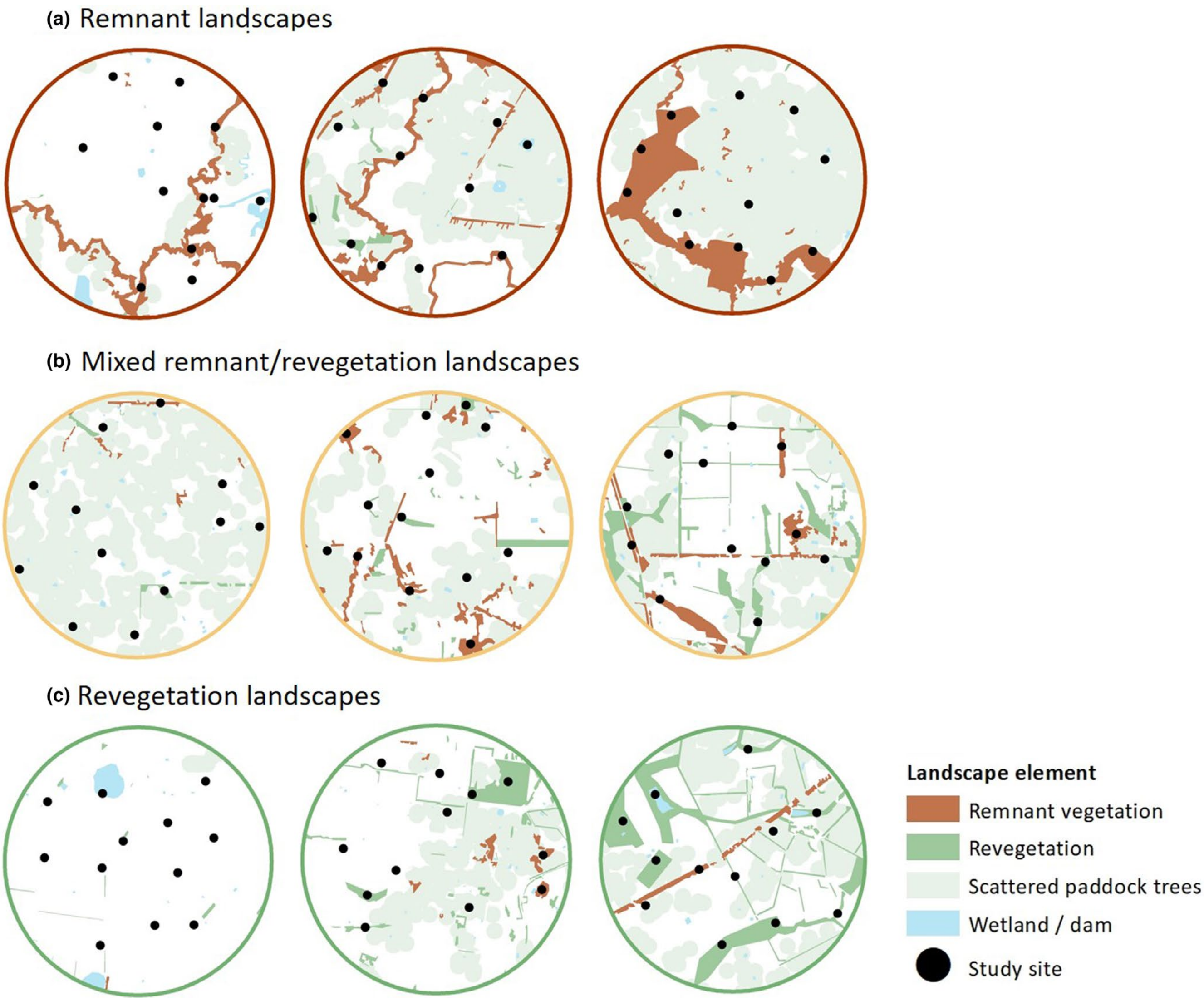

FIGURE 2 Examples of study landscapes (3.2 km diameter, 8 km^2) with increasing wooded cover (left to right): (a) 'remnant', (b) 'mixed' and (c) 'revegetation'. Survey sites in each landscape are also shown

and (c) 'mixed' landscapes ($n = 10$) including both remnant and plantings (mean proportion comprising remnant 0.49 and plantings 0.51; Appendix S1), for a total of 43 study landscapes. Each landscape was 8 km^2 in size, circular in shape and separated from others by ≥2 km. Scattered trees (mostly 200+ year old *E. camaldulensis*) among farmland are a distinctive feature (Figure 2), and so selection of landscapes sought to include a gradient in scattered tree cover in each landscape type.

Six landscape elements (i.e. land-cover classes), digitised from aerial photographs, were used for sampling: open farmland (e.g. pasture and crops); farmland with scattered trees (<2 trees per ha); remnant wooded vegetation; planted vegetation (revegetation); farm forestry (e.g. planted monocultures); and wetlands. Other elements (e.g. roads, buildings and home gardens) were a minor component not included in sampling. Scattered trees were individually digitised, a 100 m buffer was placed around each and areas comprising the intersection of five or more buffers were designated as farmland with scattered trees.

Twelve survey sites were established in each landscape (Figure 2). A single site was allocated to the largest wetland, when present. Other sites were allocated with a minimum of one per element present (and encompassing >4 ha). For wooded elements (remnants and plantings), sites were allocated in proportion to per cent cover in the landscape: 0.5%–1%, one site; 1%–2% two sites; 2%–4% three sites; 4%–7%, four sites; 7%–10%, five sites; 10%–15%, six sites; and >15%, seven sites. Farmland elements (open farmland and scattered trees) were together allocated a minimum of two sites, with further sites added when 'unallocated' sites remained after applying the rules above. Sites allocated to farmland were distributed proportionally to the ratio of farmland with or without scattered trees. Each survey site was 1 ha in size, the rectangular shape varying to ensure boundaries remained within the element of interest.

2.3 | Bird surveys

Bird surveys were conducted in accordance with wildlife research permit 10003836 from the Victorian Department of Sustainability and Environment, and Deakin University Animal Welfare Committee permit A40/2006. Surveys were conducted over a 12-month period (2006–2007) with each site surveyed in each of four seasons (i.e. 43 landscapes × 12 sites × 4 survey rounds = 2,064 surveys). All birds detected in the 1-ha site within 15 min were counted. Species detected outside the site were 'off-site' records. Two experienced observers (RC and AS) conducted all surveys, each visiting all 516 sites twice. Surveys were conducted in calm, mild weather, with timing stratified across seasons such that all sites were surveyed once each in the early morning, late morning, early afternoon and late afternoon.

We collated data at the landscape scale by pooling records across all four survey rounds (seasons), including off-site observations (within the landscape). There were two response variables per landscape: (a) the species richness of birds (across all sites and survey rounds); and (b) the reporting rate for each species, being the number of sites (out of 12) at which it was recorded (based on four survey rounds). These response variables were collated for 'all terrestrial' species (excluding exotics and species associated with aquatic habitats); and 'woodland species', those primarily associated with wooded vegetation for foraging, roosting and nesting (after Radford et al., 2005; Appendix S2). Potential bias due to variation in detectability was limited by the rigorous study design and sampling protocol, use of presence/absence data (cf. abundance) and the pooling of data across multiple sites and surveys per landscape.

2.4 | Landscape variables

Explanatory variables for each landscape (Table 1) represented: (a) total extent of wooded eucalypt vegetation (i.e. remnants and plantings); (b) aspects of the spatial configuration of wooded vegetation; (c) aspects of landscape composition; (d) distance to a potential source (remnant vegetation >500 ha); and (e) climatic variation (mean annual rainfall). Spatial variables were generated from digitised aerial photos. The number and shape of wooded patches were generated using FRAGSTATS, ver. 3.3 (McGarigal et al., 2002), and aggregation as described by Radford & Bennett (2007).

Several pairs of explanatory variables (extent of wooded vegetation vs. aggregation of wooded patches; length of watercourses vs. terrain complexity) were strongly correlated ($r > 0.65$) and so only one from each pair was included (extent of wooded vegetation and length of watercourses).

2.5 | Data analysis

1. Does landscape type influence the relationship between richness of bird species and extent of wooded cover?

We used an information theoretic approach to compare three models relating species richness (all terrestrial species and woodland species) to the extent of wooded cover (ln transformed) and landscape type:

a. Species richness ~ extent × landscape type
b. Species richness ~ extent + landscape type
c. Species richness ~ extent

Model (a) represents an interaction, such that the slope of the relationship between species richness and the extent of wooded cover differs between landscape types; (b) represents an additive effect, such that the relationship has a similar slope but intercepts differ among landscape types; and (c) represents a relationship between species richness and extent but with no influence of landscape type.

We used a linear model with Gaussian distribution for species richness, checked residuals for normality and heteroscedasticity and

TABLE 1 Landscape-level explanatory variables for each study landscape

Variable	Abbreviation	Description
Extent		
Extent of wooded vegetation (ha)	Extent[a]	Total area of wooded eucalypt vegetation, including remnant vegetation and plantings
Spatial configuration		
Number of wooded patches	NP	Number of patches of wooded vegetation, a measure of the subdivision of wooded habitats
Aggregation of wooded patches	AGG	A measure of the extent to which wooded vegetation occurs in large contiguous blocks (see Radford & Bennett 2007)
Shape of wooded patches	Shape	For each patch, shape complexity =1 − (patch area/area of smallest circumscribing circle). The mean score across all patches is a landscape-level measure of shape complexity. Higher scores represent landscapes with patches of more irregular shape
Landscape composition		
Proportion revegetation	Reveg	Proportion of all wooded vegetation comprised of plantings
Scattered trees (ha)	ST[b]	Total area of farmland with scattered tree cover. Based on a buffer of 100 m around each tree and including areas where ≥5 buffers intersect
Length of watercourses (m)	Creek	Total length (m) of watercourses in the landscape
Terrain complexity	Terrain	Measure of topographic variation based on surface area ratios for all 20 m 'cells' in a landscape. For flat terrain, the ratio equals 1. For sloping terrain, ratios are >1. The standard deviation of ratios from all cells in a landscape provides a measure of topographic variation
Distance to source		
Distance to source habitat (m)	Distance	Distance from the centre of a landscape to the edge of the nearest tract of native vegetation >500 ha
Climatic variation		
Rainfall (mm)	Rain	Average annual rainfall

[a]Ln transformation.
[b]Modelled in quadratic form.

plotted the spatial pattern of residuals (see Appendix S3). We compared models using Akaike's information criterion for small sample size (AICc). Variables were considered important if the 95% confidence limits of their coefficient did not overlap zero.

2. What are the key properties of rural landscapes that influence the richness of woodland bird species?

Here, we focussed on woodland bird species and examined factors that influenced species richness across all 43 landscapes. The five categories of explanatory variables (extent of wooded cover, spatial configuration, composition, distance to source and climatic variation; Table 1) were treated as alternative hypotheses. Models were developed to investigate all possible combinations of the five categories/hypotheses. We also hypothesised that 'total extent of wooded vegetation' and 'proportion of revegetation' may interact in a meaningful way, that is the response of woodland birds to wooded vegetation may vary depending on the proportion comprised of planted vegetation versus remnants. Thus, every model that contained both terms was duplicated to include an interaction term. In total, 39 individual models were assessed.

Species richness was normally distributed and so we used Gaussian models with an identity link function. Differences in AICc values (Δ_i) were used to compare models, and Akaike weights (w_i) for each model were computed. Variables were standardised prior to model fitting to allow direct comparison of coefficients.

3. Does the composition of the woodland bird community in 'revegetation' landscapes match that of 'remnant' landscapes?

To test for differences in the composition of woodland bird assemblages between landscape types, we first carried out an ordination of the 43 landscapes using non-metric multidimensional scaling (NMDS) and the Bray–Curtis similarity measure, based on the reporting rate of species ($n = 60$). Vectors representing the spatial and environmental attributes of each landscape (Table 1) were fitted to interpret trends.

Second, we used permutational multivariate analysis of variance (R function 'adonis') to test for differences in composition between landscape types. We first checked for homogeneity of dispersion *within* groups, using the R function 'betadisper'. This showed no difference in within-group variance across landscape types. After testing for overall differences in composition, pairwise comparisons (using Bonferroni corrections) were made among landscape types.

Third, to test for functional groups of species that contributed to assemblage differences, species were assigned to categories based on broad foraging habitat and diet (Appendix S4). We calculated the summed reporting rate across species in each category and compared these values between landscape types using a separate linear model (Gaussian distribution) for each functional group. Post hoc tests (using Bonferroni corrections) provided pairwise comparisons between landscape types. Summed reporting rate provides a measure of the frequency with which each functional group occurs in a landscape.

Analyses were undertaken in R v.4.0.0 (R Core Team, 2020) using the packages AICcmodavg v.2.2–1 (Mazerolle, 2020), emmeans v.1.7.0 (Lenth, 2021) and vegan v.2.5.7 (Oksanen et al., 2020).

3 | RESULTS

3.1 | Avifauna

A total of 122 terrestrial bird species was recorded (Appendix S2), from 11,237 species-site occurrences during the study. Ten species were recorded in all 43 landscapes, while 15 occurred in a single landscape only. Sixty species were classified as woodland species. The most common woodland species included red wattlebird *Anthochaera carunculata*, white-plumed honeyeater *Ptilotula penicillata* and brown thornbill *Acanthiza pusilla* (43, 43 and 42 landscapes respectively); while nine woodland species were recorded from a single landscape (Appendix S2). The number of species per landscape ranged from 35 to 66 for all terrestrial birds and from nine to 36 for woodland species.

3.2 | Does landscape type influence the relationship between richness of bird species and extent of wooded cover?

For all terrestrial bird species, there were two plausible models (i.e. ΔAICc < 2.0, Appendix S5). However, model outputs (Appendix S6) showed that only the extent of wooded vegetation was important (95% confidence limits do not overlap zero). Thus, the richness of terrestrial birds increased strongly with increasing extent of wooded vegetation, but this relationship did not differ between 'remnant', 'mixed' or 'revegetation' landscapes (Figure 3a). This model accounted for 59% of variation between landscapes (R^2 =0.59).

For woodland bird species, the best model included both the extent of wooded cover *and* landscape type (additive model; Figure 3b) and accounted for 60% of variation (R^2 =0.60; Appendices S5 and S6). The number of woodland species increased with the extent of

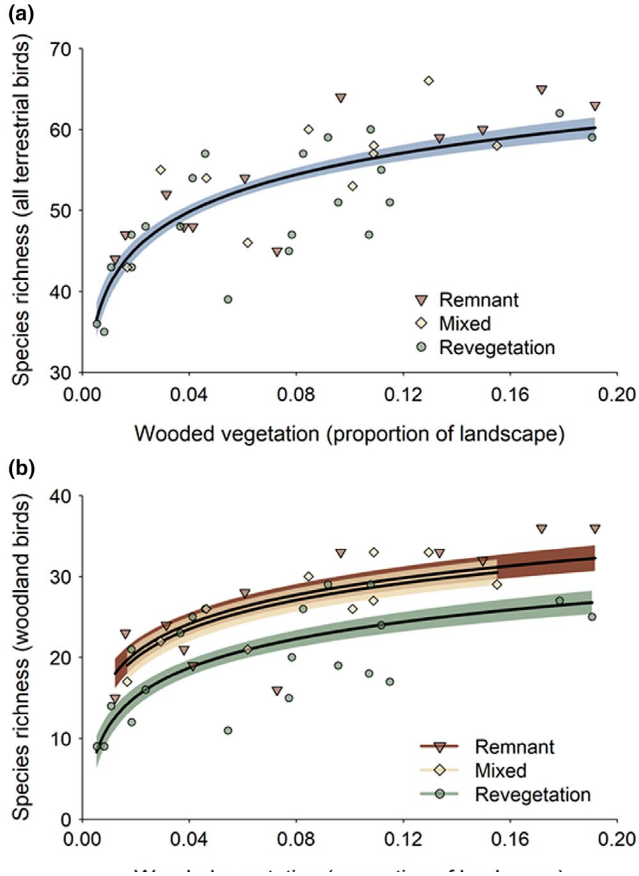

FIGURE 3 Predicted species richness of (a) all terrestrial birds and (b) woodland birds as a function of total extent of wooded vegetation in the landscape (expressed as a proportion of the landscape). Solid lines represent the fitted model, shaded areas represent ±1 *SE* and symbols show the values for individual landscapes

wooded vegetation, but for a given extent there was a greater richness in 'remnant' than 'revegetation' landscapes but no difference between 'remnant' and 'mixed' landscapes (Appendix S6).

3.3 | What are the key properties of rural landscapes that influence the richness of woodland bird species?

The best model (lowest AICc value) included variables representing three hypotheses: extent of wooded vegetation, landscape composition and climatic variation (rainfall; Appendix S7). There were seven models in the 95% confidence set (based on AIC weights) but no alternative model/s with ΔAICc < 2.0. Inspection of outputs of all models in the 95% confidence set confirmed that important variables were the extent of wooded vegetation, scattered trees in farmland, rainfall and the interaction between the extent of wooded vegetation and the proportion revegetation (Table 2). This final model accounted for 77% of the variation in woodland bird species richness between landscapes.

TABLE 2 Model of factors influencing the species richness of woodland birds in study landscapes. For description of variables, see Table 1

	Coefficient	Std. error	*p*-value	R^2 adj
Intercept	22.98	0.53	<0.001	0.77
Extent of wooded vegetation	8.38	1.43	<0.001	
Proportion revegetation	−1.64	1.57	0.302	
Scattered trees	18.40	5.26	0.001	
Scattered trees^2	−12.58	5.55	0.030	
Rainfall	2.84	1.09	0.013	
Extent wooded × Proportion revegetation	−6.60	2.38	0.009	

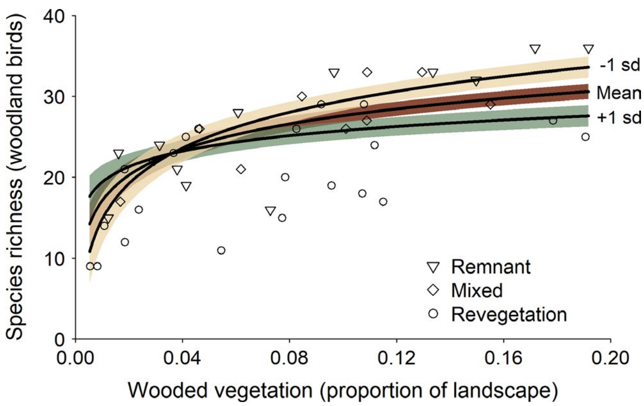

FIGURE 4 Predicted richness of woodland birds as a function of the total extent of wooded vegetation (expressed as proportion of the landscape). Predictions are shown for three values of revegetation as a proportion of wooded vegetation (mean, +1 *SD* and −1 *SD*). Shaded areas represent ±1 *SE*. Other explanatory variables (scattered trees and rainfall) were held constant at their mean value

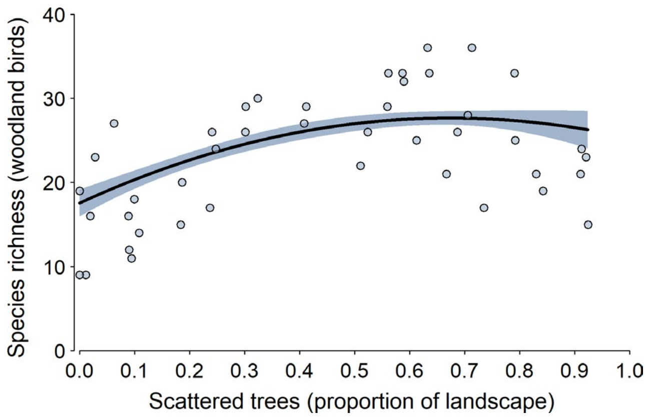

FIGURE 5 Predicted richness of woodland birds as a function of the proportion of the landscape with scattered tree cover in farmland. Shaded area represents ±1 *SE*. Other explanatory variables (rain and proportion of revegetation) were held constant at their mean value

Across all 43 landscapes, there was a significant interaction between the extent of wooded cover and the proportion comprised of revegetation plantings (Figure 4). In low-cover landscapes (e.g. <4% wooded cover), having a higher proportion of wooded cover comprised of plantings had a positive effect on richness (Figure 4). In landscapes with greater wooded cover (e.g. >10%), a higher proportion comprised of plantings resulted in lower relative richness of woodland birds (Figure 4). The richness of woodland species increased with annual rainfall (Table 2), and the area of farmland with scattered trees also had a positive influence (Figure 5) with richness increasing up to ~70% cover of scattered trees then decreasing slightly, reflecting a quadratic relationship (Table 2).

3.4 | Does the composition of the avifauna in 'revegetation' landscapes match that of 'remnant' landscapes?

Overall, there was a highly significant difference in the composition of woodland bird assemblages between landscape types (adonis, $F = 3.20$, $p < 0.001$; Appendix S8). This was primarily due to a marked difference between 'remnant' and 'revegetation' landscapes ($t = 2.301$, $p = 0.001$), with no difference between 'mixed' landscapes and other types. 'Remnant' and 'revegetation' landscapes showed clear separation in an ordination plot (Figure 6) along the first ordination axis, MDS1. Landscape variables that aligned most strongly with these compositional differences included the area of farmland with scattered trees, proportion of wooded vegetation comprised of revegetation and total extent of wooded vegetation (Figure 6).

Woodland species recorded from 'revegetation' landscapes essentially were a subset of those occurring in 'remnant' landscapes (Appendix S2); there was not a distinct suite of species associated solely with 'revegetation' landscapes. Despite greater sampling effort (21 vs. 12 landscapes), only four species occurred in 'revegetation' but not in 'remnant' landscapes, of which three were scarce (≤2/516 sites overall). Conversely, 11 species occurred in 'remnant' but not in 'revegetation' landscapes, including seven scarce species (≤2 sites).

The comparison of summed reporting rates for species in foraging categories (Figure 7, Appendix S10) showed a significantly greater reporting rate in 'remnant' than in 'revegetation' landscapes for: bark/trunk-insectivores, canopy-nectarivore/insectivores, canopy-fruits/seeds and aerial-insectivores—all groups

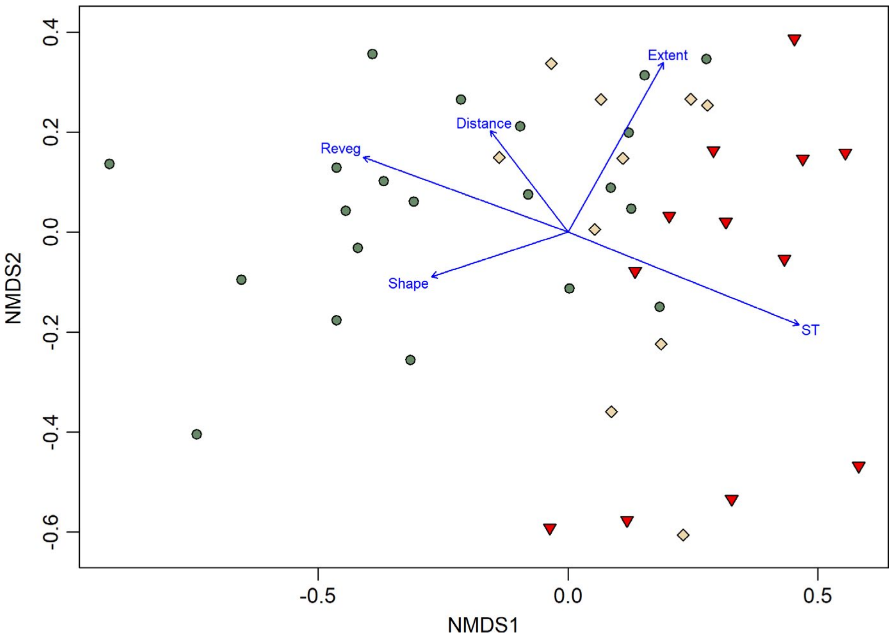

FIGURE 6 Non-metric multidimensional scaling ordination of 43 study landscapes based on the composition of the woodland bird community (stress = 0.18). Landscapes are displayed according to landscape type: 'remnant' = red triangles; 'revegetation' = green circles; and 'mixed' (remnant and revegetation) = yellow diamonds. Significant ($p < 0.05$) environmental variables are also shown (see Appendix S9). The length of the arrow indicates the strength of the correlation (for descriptions of variables, see Table 1)

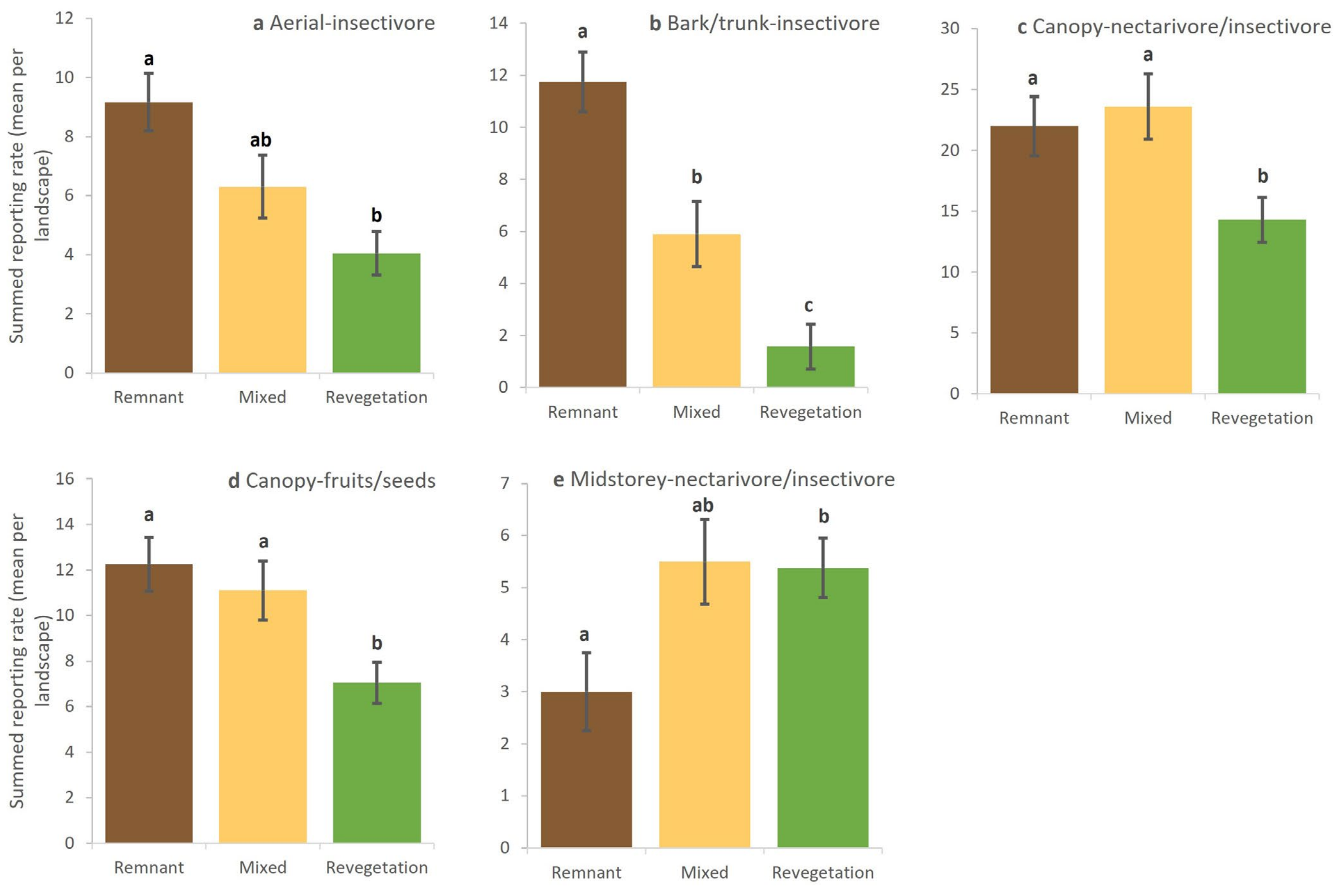

FIGURE 7 Comparison of the mean summed reporting rate of species belonging to different foraging/habitat groups in relation to landscape type. Letter codes identify landscape types identified as significantly different (differing codes) or not (matching codes) in post hoc tests (see Appendix 10). Error bars represent ±1 *SE*

associated with a mature tree layer. Of these, the reporting rate of bark/trunk-insectivores also differed between 'remnant' and 'mixed' landscapes—being higher in the former (Figure 7). For 'revegetation' landscapes, there was a greater reporting rate for midstorey-nectarivores/insectivores than in 'remnant' but not in 'mixed' landscapes (Figure 7).

4 | DISCUSSION

We evaluated the landscape-scale benefits of restoration for woodland birds by studying landscapes representing a gradient in the extent of planted wooded cover, benchmarked against landscapes with comparable extent of remnant vegetation. Restoration clearly enhanced woodland bird communities at the landscape scale, but the trajectory of community recovery was not a mirror image of the trajectory of loss. For a given extent of wooded cover, restored landscapes supported fewer species and avifaunal composition differed in predictable ways. However, 'mixed' landscapes—a combination of remnants and plantings—were similar in both richness and composition to benchmark landscapes, suggesting that restoration that bolsters landscapes with existing remnant vegetation is an effective approach to deploying restoration effort.

4.1 | Factors influencing restoration of woodland bird communities

Restoration outcomes for woodland birds were underpinned by two main processes. First, as wooded vegetation is progressively restored, species return and recolonise formerly cleared farmland as evidenced by a positive relationship between species richness and extent of wooded vegetation. That is, revegetation does not simply provide more habitat for species already present, but promotes active recolonisation that brings species back into a landscape to use newly available habitats. Where do such species come from? Our evidence suggests recolonisation occurs as 'spillover' from populations in remnant wooded vegetation in the region. Species in 'revegetation' landscapes were a subset of the regional avifauna; there was not a specialist suite that occur only in plantings. Further, at the level of individual plantings, both species richness and the occurrence of many individual species were positively influenced by the amount of nearby vegetation, at both local and broader scales (Haslem et al., 2021).

A second process supporting restoration outcomes is the selection by species of habitats that provide appropriate resources. Compositional differences between 'revegetation' and 'remnant' landscapes reflect species responding to different habitat cues. In particular, the presence of a mature tree layer, typical of many sites in 'remnant' landscapes, accounted for higher reporting rates of foraging groups that depend on resources such as bark/trunk surfaces, canopy foliage and flowers, and aerial spaces among trees. The earlier successional stages at many sites in 'revegetation' landscapes, with complex midstorey vegetation of planted shrubs and regenerating eucalypts, favoured species such as midstorey-nectarivores/insectivores.

Legacies of environmental conditions and previous land use can affect restoration outcomes by providing complementary habitats or serving as keystone structures that shape ecological processes (Manning et al., 2006). In this study, trees scattered across farmland enhanced landscape-scale richness of woodland birds and strongly influenced assemblage composition. In rural environments, scattered trees provide habitat for many species (Fischer & Lindenmayer, 2002; Haslem & Bennett, 2008) and function to 'soften' the landscape by acting as stepping stones for movement of birds and other taxa through otherwise-cleared farmland (Doerr et al., 2011). Further, plantings sited around mature trees facilitate access to resources such as large trunk and bark surfaces, tree hollows and perching sites not available in young plantings; and enhance opportunities in planted sites for many species (Barrett et al., 2008; Haslem et al., 2021).

4.2 | Landscape restoration is a dynamic process

All rural landscapes are dynamic: changes occur through time in land uses, vegetation patterns, human land-use pressures, economic conditions and environmental factors. Successional changes associated with the growth and maturation of vegetation have implications for the distribution and abundance of birds in restoration plantings and collectively for avifaunal assemblages at the landscape scale. Variation in the rate at which different plant species grow, mature and senesce determines the resources available to birds at different stages (Vesk et al., 2008; Whytock et al., 2018). Planted trees, for example, take decades to grow, mature and develop diverse resources, such as a large canopy, hollows and large limbs that fall to become logs (Vesk et al., 2008; Whytock et al., 2018).

The temporal dimension in restoration, especially time-lags in resources becoming available, is critical for restoration planning (Mac Nally, 2008; Thomson et al., 2009). In this region, plantings of native eucalypts on farms commenced in the 1970s, stimulated in subsequent decades by regional and national programs (Campbell, 1991; Hajkowicz, 2009). Plantings were a maximum of ~40 years old at the time of survey, and thus 'revegetation' landscapes primarily represented early to mid-successional vegetation. Time since planting was a significant influence on species richness and the occurrence of many species in individual plantings (Haslem et al., 2021). The complementarity of remnants and plantings in 'mixed' landscapes, which together provide resources associated with older and younger vegetation, likely explains why woodland assemblages in these landscapes did not differ in richness or composition from those in 'remnant' landscapes. We predict that with time, the maturation of plantings in 'revegetation' landscapes will result in the woodland avifauna more closely resembling that in 'remnant' landscapes.

4.3 | Implications for restoration of biodiversity in rural environments

The response of species to landscape change and their capacity for recolonisation of restored habitats varies globally among ecosystems and taxonomic groups, influenced by past habitat disturbance and degree of habitat specialisation by species (McAlpine et al., 2016;

Betts et al., 2019). The mobility of generalist bird species, for example, enhances their capacity for recolonisation, whereas for less-mobile taxa (e.g. reptiles; Michael et al., 2014) or forest specialists (Betts et al., 2019), restored habitats may be less suitable or less accessible.

Landscape-scale restoration of otherwise-cleared farmland clearly has positive outcomes for woodland birds—species of national conservation concern. Although we selected landscapes to be interspersed, a group of 'revegetation' landscapes in the south-east was associated with minor spatial clustering of residuals (Appendix S3). However, potential overprediction of modelled richness for these 'revegetation' landscapes does not alter the primary result, that 'revegetation' landscapes support lower richness than 'remnant' landscapes of similar cover. We were restricted to studying landscapes with up to 19% wooded cover as higher cover of revegetation was not available, yet such depleted environments are typical of situations where restoration is a priority. We surveyed the distribution and abundance of species over a full seasonal cycle but were not able to assess the extent of breeding within landscapes. Measures of reproductive performance provide a more reliable measure of the benefits of restoration (e.g. Belder et al., 2020), but are extraordinarily difficult to achieve when dealing with multiple species across multiple landscapes.

Time-lags in vegetation maturation and provision of resources for biota have a critical influence on restoration programs (Mac Nally, 2008; McAlpine et al., 2016). Given that the trajectory of restoration extends over decades, protection and management of existing natural vegetation provides essential resources and a framework around which plantings will, in time, add further resources. Remnant natural vegetation, even though fragmented and modified, also offers other ecosystem benefits: it is more likely to have native plants in the ground layer (e.g. grasses and herbs) and to retain diverse native biota associated with ground and soil layers (e.g. litter and soil invertebrates, fungi); and it provides a structural 'skeleton' and source of propagules from which local restoration and recolonisation can build. Similarly, sparse, scattered trees in farmland have a critical complementary role in rural landscapes.

In which landscapes will restoration efforts be most effective? The most rapid gain in landscape-scale richness of woodland birds will come from plantings in highly cleared farm landscapes—for example, increasing wooded cover from 0% to 3% of the landscape. Such rapid gains reflect the species–area relationship, whereby accumulation of species with additional habitat is most rapid at low values of habitat area (Figure 3b). However, greater strategic benefits will be achieved by employing restoration to bolster landscapes with existing, but highly depleted, remnant vegetation. Adding restoration plantings will: (a) increase the total extent of wooded habitat, with benefits for species' population sizes and increased species richness; and (b) do so in a way that provides complementary resources. Landscapes with spatial juxtaposition of both remnants and plantings provide wooded vegetation that spans multiple successional stages, thus providing complementary resources for biota. Similarly, at a patch scale, Ikin et al. (2018) concluded that complementary sets of patches of old-growth, regeneration and plantings would most effectively conserve threatened woodland birds in farmland.

Finally, restoration on farms contributes to landscape-scale biodiversity gains while also having socio-ecological and production benefits (Campbell, 1991). Revegetation plantings in this region typically have been done on a farm-by-farm basis, usually to enhance farm production rather than with nature conservation as a primary goal. Such individual actions matter, and the benefits accumulate at the landscape scale to the wider benefit of society. Nevertheless, more effective, long-term gains could be achieved by greater coordination of restoration actions at the landscape scale, to enhance both the spatial pattern and the temporal sequence of restoration actions (Thomson et al., 2009).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

A.F.B., R.H.C. and J.Q.R. conceived the ideas and designed the study; R.H.C. and A.S. collected the data; G.J.H. led data analysis supported by A.H.; A.F.B. led the writing of the manuscript. All authors contributed critically to previous versions of this work and approved its publication.

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Data available via OPAL: Open at La Trobe https://doi.org/10.26181/19236114 (Bennett et al., 2022).

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