

Riparian vegetation has disproportionate benefits for landscape-scale conservation of woodland birds in highly modified environments

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Summary

1. Identifying landscape patterns that allow native fauna to coexist with human land use is a global challenge. Riparian vegetation often persists in anthropogenic environments as strips of natural or semi-natural vegetation that provide habitat for many terrestrial species. Its relative contribution to landscape-scale conservation is likely to change as environments become increasingly modified. We used a ‘whole of landscape’ approach to test the hypothesis that riparian vegetation offers disproportionate benefits, relative to non-riparian vegetation, for the conservation of woodland birds in highly modified agricultural landscapes.

2. We selected 24 landscapes, each 100 km², along a gradient of landscape change represented by decreasing cover of native vegetation (from 60% to <2%), in an agricultural region in SE Australia. Bird species were systematically surveyed at three riparian and seven non-riparian sites in wooded vegetation in each landscape.

3. Riparian sites supported a greater richness of woodland-dependent species, a group of conservation concern, than did non-riparian sites. The composition of assemblages also differed between site types.

4. At the landscape scale, the pooled richness of bird assemblages at riparian and non-riparian sites, respectively, decreased with overall loss of tree cover despite constant sampling effort. Within landscapes, the β -diversity of woodland species among non-riparian sites increased (composition became less similar) as landscape tree cover declined. In contrast, riparian assemblages were relatively stable with no change in β -diversity. Importantly, as landscape tree cover declined, the proportion of woodland species uniquely present at riparian sites increased and made a greater contribution to overall landscape diversity.

5. *Synthesis and applications.* Landscape-scale richness of woodland species declines as landscape tree cover is lost. In highly depleted landscapes, riparian vegetation retains a relatively rich, stable assemblage compared with that in heterogeneous remnants of non-riparian vegetation and consequently contributes disproportionately to landscape-scale diversity. These observations, together with the diverse benefits of riparian vegetation for aquatic ecosystems, mean that protection and restoration of riparian vegetation is a high priority in anthropogenic environments. Importantly, such actions are directly amenable to individual land managers, and the benefits will accumulate to enhance the persistence and conservation of species at landscape and regional scales.

Key-words: agricultural environments, Australia, avifauna, β -diversity, countryside, farmland, γ -diversity, landscape, streamside, woodland birds

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Introduction

Riparian vegetation is a distinctive and ecologically important feature of landscapes throughout the world (Malanson 1993; Naiman & Decamps 1997). It has a critical role in diverse ecological processes such as filtering the flow of nutrients and pollutants into streams, regulating aquatic microclimates and providing organic input to aquatic food webs (Gregory *et al.* 1991; Naiman & Decamps 1997; Pusey & Arthington 2003). Riparian vegetation also benefits terrestrial biodiversity. Relative to the area it occupies, riparian vegetation provides habitat for a disproportionately large number of species (Redford & de Fonseca 1986; Naiman, Decamps & Pollock 1993; Knopf & Samson 1994). Plant and animal assemblages in riparian vegetation differ from those in adjacent environments, particularly those that are more arid, such that riparian zones enhance regional diversity (Sabo *et al.* 2005). Riparian vegetation may also support a greater richness and abundance of species than occurs in adjacent vegetation (Knopf & Samson 1994; Mac Nally, Soderquist & Tzaros 2000; Woinarski *et al.* 2000).

Riparian vegetation often persists in heavily modified landscapes as linear remnants of natural or semi-natural vegetation. The role and value of such remnant vegetation in maintaining assemblages of plants and animals has been widely recognized, including in agricultural landscapes (Martin *et al.* 2006; Lees & Peres 2008), urban and suburban areas (Miller *et al.* 2003; Dallimer *et al.* 2012), tree plantations (Perry *et al.* 2011) and production forests (Marczak *et al.* 2010). These results have been derived largely from site-based studies that compared the richness or composition of the biota at sites within riparian strips of different width (Hilty & Merenlender 2004; Perry *et al.* 2011) or management history (Jansen & Robertson 2001; Miller *et al.* 2003), or between riparian sites and those in adjacent non-riparian vegetation (Palmer & Bennett 2006).

The relative influence of riparian vegetation on landscape-scale patterns in biodiversity is less well known, although it is recognized as a key element in developing landscape- and regional-scale strategies for conservation (Naiman, Decamps & Pollock 1993; Knopf & Samson 1994; Woinarski *et al.* 2000). As environments become increasingly modified by humans, riparian zones may assume disproportionate importance relative to other landscape elements, due to the distinctiveness of their biota, their location in productive parts of the landscape and the potential connectivity they offer along environmental gradients (Bennett 1999; Sabo *et al.* 2005). On the other hand, riparian vegetation, as with other types of remnant vegetation, is influenced by its context and, due to its linear configuration, is exposed to edge effects that may result in simplified faunal communities (Miller *et al.* 2003; Martin *et al.* 2006) and a reduced ability to retain species in heavily modified landscapes. To draw inferences about the relative contribution of riparian vegetation to

landscape-scale conservation, it is necessary to compare riparian communities systematically across whole landscapes that have experienced different levels of anthropogenic change.

Here, we test the hypothesis that riparian vegetation has a disproportionately beneficial role, relative to non-riparian vegetation, in maintaining landscape-scale diversity of woodland birds in heavily modified landscapes. In southern Australia, the status of woodland-dependent bird species is of conservation concern with many having experienced marked declines (Ford *et al.* 2001; Martin *et al.* 2012). We used a 'whole of landscape' approach (Bennett, Radford & Haslem 2006) to assess the relative importance of riparian and non-riparian vegetation for bird species in 24 study landscapes chosen to represent a gradient in anthropogenic landscape change. We first examined assemblages at individual riparian and non-riparian sites to compare their richness and composition and to identify species that favour either site type. Then, we pooled data within landscapes for each site type to address two main questions:

1. Are the pooled species richness and the between-site diversity (β -diversity) of riparian and non-riparian assemblages, respectively, influenced by the degree of landscape modification?
2. Does the relative contribution of riparian vegetation to the landscape diversity of bird species vary along the gradient in landscape change?

Materials and methods

STUDY AREA

The study area encompasses *c.* 20 500 km² in Victoria, Australia, including parts of the inland slopes of the Great Dividing Range and the alluvial plains of the Victorian Riverina (Radford, Bennett & Cheers 2005). This region experiences hot, dry summers (mean daily maximum *c.* 30 °C) and mild winters. Mean annual rainfall (400–670 mm) increases from the NW to the SE of the region. Since European settlement in the mid-19th century, the environment has been profoundly altered by clearing for agriculture (cereal cropping, pastoralism, horticulture), logging of native forests and gold mining (ECC 1997). Less than 20% of the original extent of tree cover remains with much of this occurring on poorer soils of the inland slopes (ECC 1997).

Native vegetation of the region is dominated by eucalypt forests and woodlands (canopy height 10–25 m), with tree species composition varying in relation to topography, soils and moisture availability (ECC 1997). Dry forests dominated by grey box *Eucalyptus microcarpa*, red ironbark *E. tricarpa* and yellow gum *E. leucoxylon* are characteristic of the inland slopes, while on the lower slopes and plains, grassy woodlands dominated by grey box, yellow box *E. melliodora* and white box *E. albens* were formerly widespread but now occur as fragments. Riparian forests and woodlands along streams and floodplains are dominated by river red gum *E. camaldulensis* or, in drier environments to the north-west, by black box *E. largiflorens*. Eucalypt woodlands in both riparian and non-riparian areas have a similar open structure.

STUDY DESIGN

We selected 24 landscapes, each 10 × 10 km, that represented a gradient in tree cover (i.e. eucalypt forest and woodland) from *c.* 60% to <2% cover (Fig. 1) (see Radford, Bennett & Cheers 2005 for further details). Landscapes were selected to avoid towns and large wetlands and to minimize variation in vegetation composition and topography. In each landscape, 10 survey sites were established in remnant wooded vegetation, with at least two in each quarter of the landscape to ensure geographic spread of sampling. Three survey sites per landscape were allocated to riparian vegetation, and the remaining seven were stratified among other wooded elements – large remnants (>40 ha), small remnants (<40 ha), roadside vegetation and scattered trees – in proportion to their representation of tree cover in the landscape (Radford, Bennett & Cheers 2005). Potential sites were randomly positioned on vegetation maps, then checked in the field for suitability (e.g. access, vegetation type) and if appropriate were included.

Riparian vegetation ranges from broad stands (e.g. >100 m wide) adjacent to perennial rivers to narrow strips of trees of varying width along seasonally dry streams (typically first and second order streams). Much of the riparian vegetation is managed by private landholders through whose farms it extends, although some stream frontages (typically the larger rivers) are public land. Grazing by domestic stock (mostly sheep) is widespread, both historically and currently, and the original understory vegetation has been highly modified. In each landscape, we located one riparian site along the stream with widest riparian vegetation and the other two sites were selected (*a priori* from maps) in different quarters of the landscape. Riparian sites were sections of linear streamside strips, typically part of a remnant network of riparian vegetation among farmland.

BIRD SURVEYS

We used a fixed-width line transect of 2 ha (i.e. 400 × 50 m, or 500 × 40 m for some linear sites) to survey birds at each site

(Radford, Bennett & Cheers 2005). Each survey included a 20-min period during which all individuals detected (seen or heard) were recorded as being either 'on' or 'off' the transect. Those foraging overhead (e.g. woodswallows, raptors) were noted separately but included as on-transect. The observer then returned along the transect during a 10-min period, recording any additional species not detected during the first period. These supplementary records were regarded as off-transect. As all sites have an open woodland structure, we assumed detectability of bird species was similar between site types. Analyses were based on the presence or absence of species on transects, rather than abundance estimates.

Surveys were conducted twice each in the breeding season (October–November 2002 and 2003) and non-breeding season (March–April and June–July 2003). The order of visiting sites was rotated between survey rounds such that each site was surveyed before 10:00 on at least two occasions. For each site, the data from the four survey visits were pooled. No more than five sites from the same landscape were surveyed on the same day. Two experienced observers surveyed each site twice during the study.

In this study, we only used records of species that were detected on-transect, to ensure they were associated with a specific landscape element (e.g. riparian vegetation). We collated data for two categories of species. First, landbird species (hereafter 'landbirds') includes all species typical of north-central Victoria after excluding waterbird species and species that are vagrants or marginal to the region. Secondly, woodland-dependent species ('woodland species'), a subset of landbirds, are those associated with wooded vegetation for daily activities (foraging, roosting, nesting) and seldom observed in cleared farmland (Radford, Bennett & Cheers 2005). Nomenclature for bird species follows Christidis & Boles (2008).

DATA ANALYSES

Tree cover was used as a measure of wooded habitat. Tree cover was quantified by using a geographic information system and

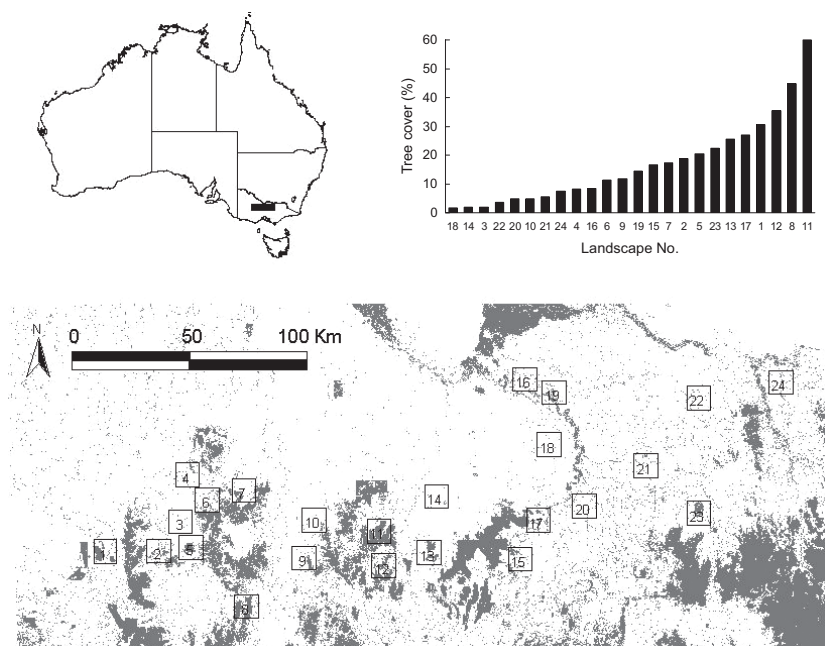


Fig. 1. The study area and study landscapes in northern Victoria (grey shading indicates tree cover) and histogram showing the variation in landscape tree cover (from Radford & Bennett 2007). The landscape number on the histogram corresponds with the label on the map.

digital tree cover map with a resolution of 10×10 m. Landscape tree cover (ha) was the summed total of all tree cover in a study landscape. Site tree cover (ha) was the summed total of all tree cover within a 250-m radius of the mid-point of each transect: this area (19.6 ha) encompassed the transect (2.0 ha) and any adjacent or nearby wooded vegetation. Both measures of tree cover were log-transformed for analyses.

At the site scale, we compared the species richness and composition of the avifauna between riparian and non-riparian sites. We used a generalized linear mixed model (GLMM), with a Poisson distribution and log link function, to model species richness of landbirds and woodland species, respectively, in relation to the fixed effect of site type (riparian vs. non-riparian) and site tree cover (ha). The latter variable was included so that differences between sites in riparian and non-riparian vegetation could be distinguished from effects associated with the amount of vegetation in close proximity to a transect. Values for site tree cover were centred (mean = 0) and standardized by dividing by two standard deviations to allow direct comparison of the relative effects of site type and tree cover on species richness (Gelman 2008). Landscape was incorporated as a random factor to account for spatial clustering of sites in study landscapes. An additional, site-level random effect was included to account for further variance in the data than assumed by a Poisson distribution (Zuur, Ieno & Saveliev 2012). Model fit was assessed by using the marginal coefficient of determination ($R^2_{\text{GLMM}(m)}$) (Nakagawa & Schielzeth 2013). GLMMs were fitted using the lme4 package (Bates, Maechler & Bolker 2012).

To compare the composition of assemblages between sites in riparian and non-riparian vegetation, we adopted a model-based approach for multivariate analysis, using the package mvabund (Wang *et al.* 2012). This approach fits a separate generalized linear model for each species, allowing the mean–variance relationships of multivariate data to be modelled more accurately than techniques based on a matrix of pairwise measures such as Bray–Curtis index (Warton, Wright & Wang 2012). It then uses resampling-based hypothesis testing to make community-level and taxon-specific inference about which predictors have significant influence (Wang *et al.* 2012). Analyses were undertaken separately for landbirds and woodland species, to test whether there were compositional differences in assemblages in relation to two predictor variables, site type (riparian vs. non-riparian) and site tree cover. A binomial distribution was specified to model the presence/absence of each species at each site, and the Wald statistic was used as the test statistic. Multivariate *P*-values were calculated to assess compositional differences in relation to site type and site tree cover, based on 500 resamples using parametric bootstrapping (Wang *et al.* 2012). Univariate *P*-values were calculated to identify individual species that showed significant relationships with predictors. *P*-values were adjusted for multiple testing across species (Wang *et al.* 2012).

At the landscape scale, we compared the avifaunal assemblages of riparian and non-riparian sites in three ways. First, we collated the pooled richness (γ -diversity) of landbirds and woodland species, respectively, for the three riparian sites and for three randomly selected, non-riparian sites in the same landscape. To avoid bias in selection of three non-riparian sites, we calculated the mean pooled richness of all possible combinations of three sites in each landscape ($n = 35$). We used GLMs with a Gaussian

distribution and identity link function to examine the relationship between γ -diversity and landscape tree cover separately for each site type. Location of each landscape (easting) was included to control for geographic variation, known to influence assemblages (Radford, Bennett & Cheers 2005). Values for landscape tree cover and easting were standardized to allow direct comparisons of coefficients.

Secondly, we calculated between-site diversity (β -diversity) for assemblages at riparian and non-riparian sites, respectively, in each landscape by using the asbio package (Aho 2013). We used the classical Whittaker measure for β diversity (Whittaker 1960; Anderson *et al.* 2011), where:

$$\beta \text{ diversity} = (\gamma\text{-diversity}/\text{mean } \alpha\text{-diversity}).$$

For example, for riparian vegetation, β diversity was calculated for each landscape by dividing the pooled richness (γ diversity) of the three riparian sites by the mean richness (α -diversity) of individual riparian sites. Beta diversity was then modelled, separately for each site type, in relation to landscape tree cover (controlling for geographic location) by using GLMs with identity link function.

Thirdly, we assessed the contribution of riparian vegetation to overall landscape diversity by using two complementary indices (Sabo & Soykan 2006).

1. The proportion of unique riparian species (R_u) is the number of species recorded only in riparian sites, as a proportion of the total landscape assemblage. It is given by:

$$R_u = a/(a + b + c),$$

where a and b are the number of species unique to riparian and non-riparian sites, respectively, and c is the number of species shared by the two site types.

2. The proportional increase in the landscape assemblage due to riparian sites (R_{add}) is the number of species unique to riparian sites as a proportion of the total species recorded at non-riparian sites. It is given by:

$$R_{\text{add}} = a/(b + c)$$

For each measure, we used regressions to model the relationship with landscape tree cover, controlling for geographic location (easting), to test the hypothesis that riparian vegetation makes a disproportionately greater contribution at lower tree cover. As the proportion of unique riparian species (R_u) is a true proportion, bound at zero and one, we used beta regression models with a logit link function (Ferrari & Cribari-Neto 2004), generated using the betareg package (Cribari-Neto & Zeileis 2010). To model the proportional increase in the landscape assemblage (R_{add}), we used a GLM with identity link function, as in this case the number of unique species is expressed as a proportion of the richness of a separate assemblage (i.e. of pooled non-riparian sites) and therefore is not a true proportion (i.e. it can exceed one). Landscape-scale models were checked for spatial autocorrelation using Moran's *I* test statistic at all neighbourhood distances. No significant spatial autocorrelation was found at any neighbourhood distance for the response variables after correcting for multiple comparisons (see Appendix S2, Supporting information).

All analyses were undertaken in R (version 2.11.1) (R-Development Core Team 2010). Variables were regarded as having a significant influence on the response variable when the 95% confidence interval of the coefficient did not overlap with zero.

Results

In total, 126 species of landbirds, including 76 woodland species, were recorded on transects during the study. Most species occurred at sites in both riparian and non-riparian vegetation: 83% of landbird species (104/126) and 82% of woodland species (62/76) were recorded at riparian sites, while for non-riparian sites comparable figures were 92% and 91%, respectively. The frequency of occurrence of all species, at both site and landscape scales, is given in Appendix S1 (Supporting Information). One nationally threatened species (swift parrot *Lathamus discolor*, endangered) was recorded in 11 landscapes; many other species (e.g. grey-crowned babbler *Pomatostomus temporalis*, diamond firetail *Stagonopleura guttata*, speckled warbler *Chthonicola sagittata*), though not nationally threatened, are of conservation concern (Ford *et al.* 2001; Mac Nally *et al.* 2009).

COMPARISONS AT THE SITE SCALE

The species richness of all landbirds and woodland species differed between site types and increased with increasing site tree cover (Table 1). For a given level of site tree cover, riparian sites supported a greater richness than non-riparian sites, with this disparity more marked for all landbirds than for woodland species.

The composition of landbird and woodland bird assemblages differed significantly between riparian and non-riparian sites (landbirds, Wald statistic = 26.38, $P = 0.001$; woodland species, Wald = 17.37, $P = 0.001$), and also in relation to site tree cover (landbirds, Wald statistic = 26.63, $P = 0.001$; woodland species, Wald = 21.52, $P = 0.001$). Differences in composition were driven primarily by species that favoured riparian vegetation (Appendix S1, Supporting information). This included woodland species such as the sacred kingfisher *Todiramphus sanctus*, superb fairy-wren *Malurus cyaneus*, and white-plumed honeyeater *Lichenostomus penicillatus*, as well as landbird species such as rufous songlark *Cincloramphus mathewsi* and sulphur-crested cockatoo *Cacatua*

Table 1. Results from generalized linear mixed models of the relationship between species richness and site type (riparian, non-riparian vegetation), controlling for site tree cover. For site type, the reference category is non-riparian vegetation. Landscape was included as a random factor. Coefficients, z -values (coefficient/standard error) and variance explained (R^2) are given for each model

Response	Model term	Coefficient	z -value	$R^2_{\text{GLMM(m)}}$
Landbird species	Site tree cover (log)	0.272	7.65	38.1
	Site type: riparian	0.336	10.42	
Woodland species	Site tree cover (log)	0.965	13.13	51.3
	Site type: riparian	0.355	5.86	

galerita. Compositional differences were also influenced by woodland species associated with non-riparian vegetation (e.g. brown-headed honeyeater *Melithreptus brevirostris*, rufous whistler *Pachycephala rufiventris*) (Appendix S1, Supporting information).

COMPARISONS AT THE LANDSCAPE SCALE

Pooled species richness of assemblages at riparian and non-riparian sites showed similar trends: richness of both landbirds and woodland species decreased as landscape tree cover decreased (Table 2, Fig. 2). When comparing just the univariate relationship between pooled species richness and landscape tree cover, the fit of the model differed substantially between site types: R^2 values for riparian sites were 12.6% for landbirds and 19.1% for woodland species, while for non-riparian sites it was 48.3% for landbirds and 55.6% for woodland species. Thus, as landscape tree cover is lost, there is a stronger relationship (size of the coefficient, Table 2) and more variance in richness is explained (R^2 values) for non-riparian sites than for riparian sites.

Patterns of β -diversity for riparian and non-riparian sites showed contrasting responses to landscape change. For riparian sites, β -diversity was not related to landscape tree cover or geographic location (easting), either for landbirds or woodland species (Table 3, Fig. 3). That is, the average contribution of individual riparian sites to the pooled richness of assemblages in riparian vegetation in each landscape did not change significantly as tree cover declined. In contrast, for non-riparian sites, β -diversity of landbirds was positively related to landscape tree cover, while β -diversity of woodland species was negatively related to landscape tree cover (Table 3, Fig. 3). Thus, for non-riparian sites, as landscape tree cover decreased, there was less variation between sites for landbirds, but more variation between sites for woodland species (Fig. 3).

In each landscape, riparian sites supported numerous 'unique' species not recorded at non-riparian sites in that

Table 2. Models of the relationship between pooled species richness at riparian and non-riparian sites, respectively, in each landscape in relation to landscape tree cover. Coefficients and t -values (coefficient/standard error) are given for each model

Response	Predictors	Riparian		Non-riparian	
		Coefficient	t -value	Coefficient	t -value
Landbirds	Landscape tree cover (log)	3.45	2.38	4.33	3.32
	Easting	3.07	2.11	-2.10	3.01
Woodland species	Landscape tree cover (log)	3.97	4.20	5.24	4.91
	Easting	3.59	-2.03	-1.99	-1.86

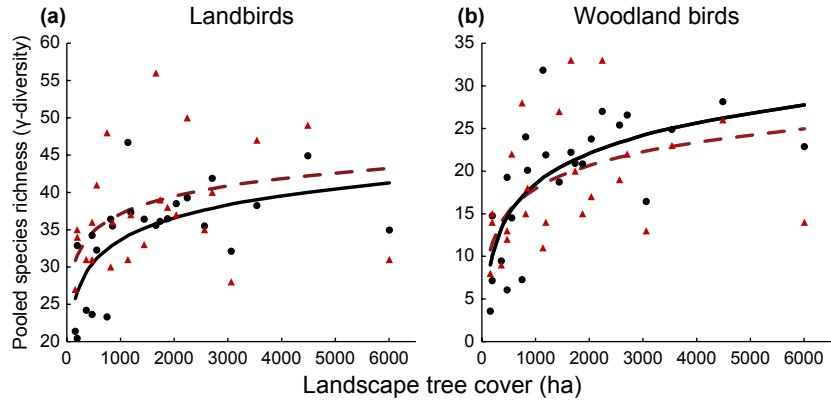


Fig. 2. Relationship between pooled species richness for landbirds and woodland species, respectively, in study landscapes in relation to landscape tree cover. Fitted models and raw data are shown for riparian (dashed lines, triangles) and non-riparian vegetation (solid lines, circles).

Table 3. Models of the relationship between β -diversity of bird species for riparian and non-riparian sites and landscape tree cover, controlling for geographic location (easting). Coefficients, t -values and variance explained (R^2) are given for each model

Response	Variable	Riparian sites			Non-riparian sites		
		Coefficient	t -value	R^2	Coefficient	t -value	R^2
Landbirds	Landscape tree cover (log)	0.028	0.846	0.039	0.171	3.128	0.318
	Easting	0.019	0.568		0.037	0.671	
Woodland species	Landscape tree cover (log)	0.035	0.881	0.060	-0.206	-2.593	0.541
	Easting	0.038	0.950		0.277	3.485	

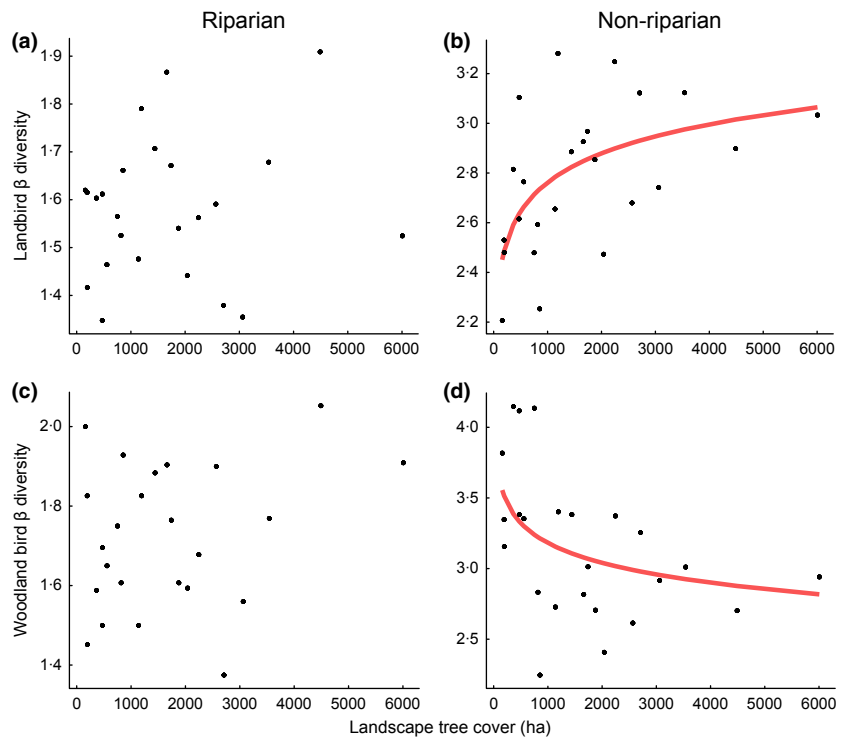


Fig. 3. Relationship between β -diversity and landscape tree cover (ha) for landbirds at (a) riparian and (b) non-riparian sites, and for woodland species at (c) riparian and (d) non-riparian sites in 24 study landscapes. Fitted lines show the predicted values for significant relationships (solid circles represent observed values for each landscape).

landscape. For landbirds, a mean of 10.2 (range 5–27) species per landscape occurred uniquely at riparian sites, representing on average 17.2% of the landscape assemblage. For woodland species, a mean of 5.6 species (range 0–22) per landscape, or 18.0% of the woodland species assemblage,

occurred uniquely at riparian sites. Species consistently occurring as unique (i.e. in ≥ 5 landscapes) included 13 species of landbird (of which eight were woodland species), most significantly associated with riparian vegetation (Appendix S1, Supporting information).

The proportion of unique riparian species (R_u) varied geographically with a greater proportion in landscapes to the east (Table 4). For woodland species, there was a significant negative relationship with landscape tree cover (Table 4, Fig. 4a). Thus, in depleted low-cover landscapes, riparian vegetation supported a proportionally larger number of unique woodland species, not otherwise recorded in the landscape. For landbirds, there was a similar, but non-significant relationship (Table 4).

The percentage increase in the landscape assemblage (R_{add}) due to species unique to riparian sites ranged from 4.3 to 79.4% (mean = 22.2%) for landbirds, and for woodland species 0.0 to 169.2% (mean = 27.3%). One landscape (Black Dog Creek) was an outlier, particularly for woodland species, with a percentage increase (169.2%) more than four standard deviations from the mean. It was excluded from further analyses. Variation among landscapes in the percentage increase due to riparian sites was positively related to easting (Table 4). For woodland species, it was negatively related to landscape tree cover (Table 4, Fig. 4b), while for landbirds a similar but non-significant trend was evident. Hence, riparian sites added proportionally more to landscape richness in those landscapes that had experienced greater loss of tree cover.

Discussion

We used a 'whole of landscape' approach to examine the value of riparian vegetation to the landscape-scale conservation of bird assemblages in modified agricultural environments. A key finding was that riparian vegetation enhanced diversity at the landscape scale by supporting

unique species additional to those recorded in non-riparian vegetation. This contribution was relatively greater in the most depleted landscapes, consistent with the hypothesis that riparian vegetation has disproportionate benefits for conservation in highly modified environments.

RIPARIAN VEGETATION – SITE SCALE

In our study area, riparian sites supported both more and different species compared with non-riparian sites. A greater species richness of woodland birds at riparian sites has also been observed in other studies (e.g. Mac Nally, Soderquist & Tzaros 2000; Palmer & Bennett 2006) but is not necessarily true in all situations (McGarigal & McComb 1992). Compositional differences, however, consistently occur for a wide range of taxa across multiple continents (Sabo *et al.* 2005).

While woodland bird species are of conservation concern in southern Australia (Ford *et al.* 2001), the value of riparian vegetation for other species is also important. First, a number of other landbird species were strongly associated with riparian vegetation (Appendix S1, Supporting information). Secondly, other landbirds are also vulnerable to environmental change: notably, they were equally represented with woodland species among the two-thirds of species that experienced regional decline associated with a decade of severe drought (Mac Nally *et al.* 2009). Thirdly, common species have an important place in shaping ecosystems, through their contribution to the structure of communities and role in ecological interactions (Gaston & Fuller 2008). Finally, such species include many common birds that landholders regularly

Table 4. Models of the contribution of riparian sites to landscape richness in relation to landscape tree cover, controlling for geographic location (easting). Two indices were used: (a) the proportion of unique riparian species (R_u) and (b) the proportional increase in the landscape assemblage (R_{add}). See Materials and methods for further details

Response	Predictors	Proportion unique riparian (R_u)			Proportional increase (R_{add})		
		Coefficient	<i>z</i> -value	R^2	Coefficient	<i>t</i> -value	R^2
Landbirds	Tree cover	-0.127	-1.576	0.53	-0.025	-0.947	0.40
	Easting	0.334	4.099		0.088	3.316	
Woodland species	Tree cover	-0.395	-2.843	0.31	-0.077	-3.109	0.59
	Easting	0.757	5.220		0.095	3.548	

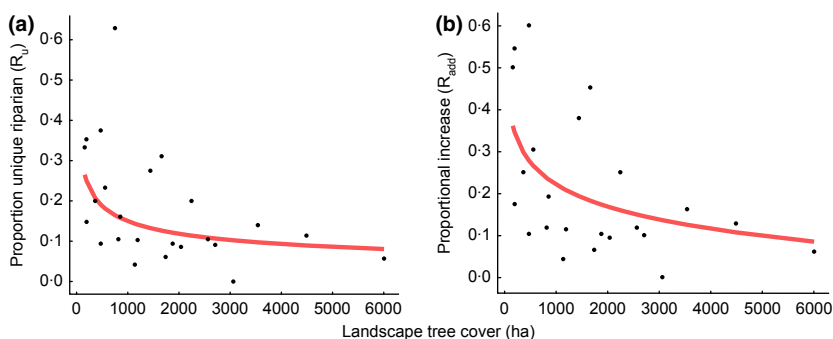


Fig. 4. Relationship between (a) proportion of unique riparian species (R_u) and (b) proportional increase in landscape assemblages due to riparian sites (R_{add}), and landscape tree cover (ha) for woodland species. The fitted lines show predicted values; solid circles represent observed values for each landscape.

encounter, including iconic species such as the laughing kookaburra *Dacelo novaeguineae*, and are important in motivating conservation efforts on private land.

RIPARIAN VEGETATION – LANDSCAPE SCALE

There were two notable patterns at the landscape scale. First, as landscape tree cover was lost, the pooled richness of bird assemblages declined, despite a constant sampling effort in each landscape. This relationship was stronger for assemblages in non-riparian vegetation than in riparian vegetation. Thus, the bird assemblages of riparian vegetation in the study landscapes were less sensitive to the changing landscape context. Secondly, for woodland bird species, as landscape tree cover declined, assemblages in riparian vegetation made a proportionally greater contribution to the overall landscape diversity of woodland species. That is, there were proportionally more species unique to riparian sites in the more depleted landscapes. A similar, but non-significant, trend was also evident for all landbirds.

The mechanism for this disproportionate contribution of riparian vegetation in highly modified landscapes was revealed by patterns of β -diversity in the study landscapes, which differed markedly between riparian and non-riparian sites. For riparian sites, β -diversity of both woodland species and landbirds did not vary significantly along the gradient in landscape tree cover. In both low-cover and high-cover landscapes, the average contribution of individual riparian sites to the pooled richness of birds in riparian vegetation did not differ.

In contrast, for non-riparian sites, β -diversity displayed significant but opposite trends for all landbirds and woodland species as landscape tree cover declined. With decreasing tree cover, β -diversity of landbirds became lower (i.e. assemblages more similar), while for woodland species it became higher (assemblages less similar). These results can be attributed to greater heterogeneity of non-riparian sites in depleted landscapes. Non-riparian sites included large and small remnants, roadsides and scattered trees. With decreasing landscape tree cover, wooded vegetation became dominated by small remnants, roadsides and scattered trees – and sample sites were allocated accordingly (Radford, Bennett & Cheers 2005). Generalist species that tolerate or favour modified environments persist in the landscape despite increasing change, whereas woodland specialists occur at fewer and fewer sites. Thus, there is a homogenization of the overall landbird community in non-riparian vegetation due to the prevalence of generalist species (i.e. β -diversity decreases), but concurrently, there is an increase in between-site variability of woodland species (i.e. β -diversity increases) as they become increasingly rare and thereby stochastic in their occurrence.

Overall, the key role of riparian vegetation in highly modified environments can be attributed to the relatively higher species richness and consistency of assemblages

between sites, contrasting with non-riparian sites which become increasingly dominated by impoverished assemblages of generalist species associated with more heterogeneous landscape elements. Consequently, in depleted landscapes, the proportion of species unique to riparian vegetation is higher and the proportional contribution to landscape diversity is greater. However, not all species regularly occur in riparian vegetation: many woodland species are more strongly associated with non-riparian woodlands, which have a complementary role in maintaining the overall assemblage.

In what way does riparian vegetation differ from non-riparian vegetation that accounts for the disproportionate benefits it provides? Riparian vegetation occurs in productive parts of the landscape on more fertile soils with greater availability of water, resulting in greater structural complexity of the vegetation and more reliable and abundant food resources (e.g. nectar, seeds, invertebrates) (Woinarski *et al.* 2000; Palmer & Bennett 2006). Riparian vegetation frequently has large old trees, which in turn give rise to tree hollows and coarse woody debris (e.g. Mac Nally, Soderquist & Tzaros 2000), which provide nesting and foraging resources used by many bird species.

It is important to recognize several caveats associated with this study. First, the riparian sites were remnants, typically surrounded by cleared farmland used for grazing stock or cropping. Some were broad swathes on public land adjacent to rivers, and many were narrow strips through farmland, but they were not riparian zones embedded within continuous dryland forest. In the latter situation, riparian vegetation will have greater value for woodland species as it is not exposed to farmland edges and there is greater opportunity for movement between adjacent riparian and non-riparian habitats. Consequently, it is likely that this study has underestimated the potential contribution of riparian vegetation to landscape diversity.

Secondly, we did not incorporate in analyses the variation among sites associated with land management and habitat attributes (e.g. density and size of trees, ground layer complexity), which reflect variation in habitat quality. These attributes may explain further variation in patterns of occurrence of species (Mac Nally, Soderquist & Tzaros 2000; Jansen & Robertson 2001).

Thirdly, our aim was to examine the relative contribution of riparian vegetation to avifaunal conservation along a gradient of anthropogenic land use. We systematically surveyed and compared assemblages from a fixed number of sites in riparian and non-riparian vegetation, in landscapes representing a gradient of decreasing tree cover. The absolute contribution of riparian vegetation to landscape diversity is likely to be influenced by additional factors, for example the total area of riparian vs. non-riparian vegetation, the connectivity of riparian vegetation, and the number of streams and their spatial arrangement in the landscape. Riparian vegetation is subject to more stringent controls in relation

to logging and tree clearance, such that as total tree cover declines, the proportion of the total vegetation accounted for by riparian vegetation increases. Thus, the absolute contribution of riparian vegetation is likely to be greater than the relative contribution reported in this study.

IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

Globally, the conservation of biodiversity depends fundamentally on the extent to which species can persist within human-dominated environments – particularly agricultural lands which increasingly dominate Earth's surface (Foley *et al.* 2005). Much attention has been given to factors that influence the persistence of species in agricultural landscapes: for example, the importance of heterogeneity (Benton, Vickery & Wilson 2003), keystone structures (Tews *et al.* 2004), connectivity (Bennett 1999), and the extent and pattern of native vegetation (Bennett, Radford & Haslem 2006). Riparian vegetation not only contributes to each of these themes, but has a critical role in ecological processes linking aquatic and terrestrial environments and the provision of ecosystem services for humans (Gregory *et al.* 1991; Naiman & Decamps 1997). Consequently, the protection, management and restoration of riparian vegetation is a high priority in conservation strategies for anthropogenic environments.

A key point is that the management and restoration of riparian vegetation is amenable to the scale of action of individual land managers or community groups, and their combined actions will have cumulative benefits at the landscape or catchment scale. Three types of measures can be readily identified. First, increasing the width of riparian vegetation will increase the richness of assemblages (Hilty & Merenlender 2004; Lees & Peres 2008; this study). Increased width can be achieved by restoring adjacent vegetation, infilling vegetation across bends in streams or by *a priori* planning to retain wide strips. Secondly, enhancing the connectivity of riparian vegetation for terrestrial biota can be achieved by preventing 'breaks' in vegetated strips or by restoration to fill such 'gaps'. Thirdly, managing the composition and structure of riparian vegetation can increase its quality as faunal habitat: for example, by controlling degrading processes such as intensive stock grazing (Jansen & Robertson 2001) and by promoting structural complexity (e.g. large trees, logs, vegetation heterogeneity).

Acknowledgements

We thank Garry Cheers for major contributions to bird surveys, many landholders for access to their properties, and Department of Sustainability and Environment and Parks Victoria (Research Permit 10002099) for permission to conduct research in state forests and parks. Thanks to David Warton for advice on the mvabund package. Funding was received from Land and Water

Australia (Project DUV06) and the Department of Sustainability and Environment. The manuscript was written while AFB was a Bullard Fellow at Harvard Forest, Harvard University, for which he is most grateful. We thank two anonymous referees and the editor for valuable comments.

References

- Aho, K. (2013) *asbio: a collection of statistical tools for biologists. R package version 0.4-11*. <http://CRAN.R-project.org/package=asbio>.
- Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L. *et al.* (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters*, **14**, 19–28.
- Bates, D., Maechler, M. & Bolker, D. (2012) *lme4: linear mixed-effects models using Eigen and Eigen++*. R package version 0.999999-0. <http://CRAN.R-project.org/package=lme4>.
- Bennett, A.F. (1999) *Linkages in the Landscape. The Role of Corridors and Connectivity in Wildlife Conservation*. IUCN-The World Conservation Union, Gland, Switzerland.
- Bennett, A.F., Radford, J.Q. & Haslem, A. (2006) Properties of land mosaics: implications for nature conservation in agricultural environments. *Biological Conservation*, **133**, 250–264.
- Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution*, **18**, 182–188.
- Christidis, L. & Boles, W. (2008) *Systematics and Taxonomy of Australian Birds*. CSIRO Publishing, Collingwood, Australia.
- Cribari-Neto, F. & Zeileis, A. (2010) Beta regression in R. *Journal of Statistical Software*, **34**, 1–24.
- Dallimer, M., Rouquette, J.R., Skinner, A.M.J., Armsworth, P.R., Maltby, L.M., Warren, P.H. & Gaston, K.J. (2012) Contrasting patterns in species richness of birds, butterflies and plants along riparian corridors in an urban landscape. *Diversity and Distributions*, **18**, 742–753.
- ECC (1997) *Box-Ironbark Forests and Woodlands Investigation. Resources and Issues Report*. Environment Conservation Council, Melbourne, Australia.
- Ferrari, S. & Cribari-Neto, F. (2004) Beta regression for modelling rates and proportions. *Journal of Applied Statistics*, **31**, 799–815.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C. *et al.* (2005) Global consequences of land use. *Science*, **309**, 570–574.
- Ford, H.A., Barrett, G.W., Saunders, D.A. & Recher, H.F. (2001) Why have birds in the woodlands of Southern Australia declined? *Biological Conservation*, **97**, 71–88.
- Gaston, K.J. & Fuller, R.A. (2008) Commonness, population depletion and conservation biology. *Trends in Ecology & Evolution*, **23**, 14–19.
- Gelman, A. (2008) Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine*, **27**, 2865–2873.
- Gregory, S.V., Swanson, F.J., McKee, W.A. & Cummins, K.W. (1991) An ecosystem perspective of riparian zones. *BioScience*, **41**, 540–551.
- Hilty, J.A. & Merenlender, A.M. (2004) Use of riparian corridors and vineyards by mammalian predators in Northern California. *Conservation Biology*, **18**, 126–135.
- Jansen, A. & Robertson, A.I. (2001) Riparian bird communities in relation to land management practices in floodplain woodlands of south-eastern Australia. *Biological Conservation*, **100**, 173–185.
- Knopf, F.L. & Samson, F.B. (1994) Scale perspectives on avian diversity in western riparian ecosystems. *Conservation Biology*, **8**, 669–676.
- Lees, A.C. & Peres, C.A. (2008) Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. *Conservation Biology*, **22**, 439–449.
- Mac Nally, R., Soderquist, T.R. & Tzaros, C. (2000) The conservation value of mesic gullies in dry forest landscapes: avian assemblages in the box-ironbark ecosystem of southern Australia. *Biological Conservation*, **93**, 293–302.
- Mac Nally, R., Bennett, A.F., Thomson, J.R., Radford, J.Q., Unmack, G., Horrocks, G. & Vesk, P.A. (2009) Collapse of an avifauna: climate change appears to exacerbate habitat loss and degradation. *Diversity and Distributions*, **15**, 720–730.
- Malanson, G.P. (1993) *Riparian Landscapes*. Cambridge University Press, Cambridge.
- Marczak, L.B., Sakamaki, T., Turvey, S.L., Deguise, I., Wood, S.L.R. & Richardson, J.S. (2010) Are forested buffers an effective conservation

- strategy for riparian fauna? An assessment using meta-analysis. *Ecological Applications*, **20**, 126–134.
- Martin, T.G., McIntyre, S., Catterall, C.P. & Possingham, H.P. (2006) Is landscape context important for riparian conservation? Birds in grassy woodland. *Biological Conservation*, **127**, 201–214.
- Martin, T.G., Catterall, C.P., Manning, A.D. & Szabo, J.K. (2012) Australian birds in a changing landscape: 220 years of European colonisation. *Birds and Habitat: Relationships in Changing Landscapes* (ed. R.J. Fuller), pp. 453–480. Cambridge University Press, Cambridge.
- McGarigal, K. & McComb, W.C. (1992) Streamside versus upslope breeding bird communities in the central Oregon Coast Range. *Journal of Wildlife Management*, **56**, 10–23.
- Miller, J.R., Wiens, J.A., Hobbs, N.T. & Theobald, D.M. (2003) Effects of human settlement on bird communities in lowland riparian areas of Colorado (USA). *Ecological Applications*, **13**, 1041–1059.
- Naiman, R.J. & Decamps, H. (1997) The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics*, **28**, 621–658.
- Naiman, R.J., Decamps, H. & Pollock, M. (1993) The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications*, **3**, 209–212.
- Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133–142.
- Palmer, G.C. & Bennett, A.F. (2006) Riparian zones provide for distinct bird assemblages in forest mosaics of southeast Australia. *Biological Conservation*, **130**, 447–457.
- Perry, R., Wigley, T., Melchior, M., Thill, R., Tappe, P. & Miller, D. (2011) Width of riparian buffer and structure of adjacent plantations influence occupancy of conservation priority birds. *Biodiversity and Conservation*, **20**, 625–642.
- Pusey, B.J. & Arthington, A.H. (2003) Importance of the riparian zone to the conservation and management of freshwater fish: a review. *Marine and Freshwater Research*, **54**, 1–16.
- Radford, J.Q. & Bennett, A.F. (2007) The relative importance of landscape properties for woodland birds in agricultural environments. *Journal of Applied Ecology*, **44**, 737–747.
- Radford, J.Q., Bennett, A.F. & Cheers, G.J. (2005) Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation*, **124**, 317–337.
- R-Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Redford, K. & de Fonseca, G. (1986) The role of gallery forests in the zoogeography of the Cerrado's non-volant mammal fauna. *Biotropica*, **18**, 126–135.
- Sabo, J.L. & Soykan, C.U. (2006) Riparian zones increase regional richness by supporting different, not more, species: reply. *Ecology*, **87**, 2128–2131.
- Sabo, J.L., Sponseller, R., Dixon, M., Gade, K., Harms, T., Heffernan, J. *et al.* (2005) Riparian zones increase regional species richness by harboring different, not more, species. *Ecology*, **86**, 56–62.
- Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwaiger, M. & Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, **31**, 79–92.
- Wang, Y., Naumann, U., Wright, S.T. & Warton, D.I. (2012) mvabund—an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution*, **3**, 471–474.
- Warton, D.I., Wright, S.T. & Wang, Y. (2012) Distance-based multivariate analyses confound location and dispersion effects. *Methods in Ecology and Evolution*, **3**, 89–101.
- Whittaker, R.H. (1960) Vegetation of the Siskiyou mountains, Oregon and California. *Ecological Monographs*, **30**, 279–338.
- Woinarski, J.C.Z., Brock, C., Armstrong, M., Hempel, C., Cheal, D. & Brennan, K. (2000) Bird distribution in riparian vegetation in the extensive natural landscape of Australia's tropical savanna: a broad-scale survey and analysis of a distributional data base. *Journal of Biogeography*, **27**, 843–868.
- Zuur, A.F., Ieno, E.N. & Saveliev, A.A. (2012) *Zero Inflated Models and Generalized Linear Mixed Models with R*. Highland Statistics Ltd., Newburgh, UK.

Received 17 July 2013; accepted 26 November 2013

Handling Editor: J. Wilson

Supporting Information

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

Appendix S1. Summary of all landbirds and woodland-dependent species and their frequency of occurrence in riparian and non-riparian sites.

Appendix S2. Summary of *P*-values for Moran's *I* tests for spatial autocorrelation of response variables at multiple neighbourhood distances.