# The stability of bird assemblages across time and the reliability of snapshot surveys

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## Abstract

'Snapshot' surveys conducted over 1 year or less are widely used to describe avian community composition. Maron et al. (*Austral Ecology*, 2005, 30, 383) questioned the utility of snapshot surveys and the conclusions drawn from them following repeat bird surveys at 26 sites in western Victoria, 7 years after initial surveys. They concluded, 'the distribution of most species did not differ significantly from that expected if species had redistributed at random among sites'. Only five of 54 species recorded in both years had distributions that changed significantly less than expected among sites between the survey periods. We question whether this is the exception rather than the rule for Australian landbird communities in wooded habitats for three reasons: (1) passerine species dominate these communities and tend to remain faithful to a site once a breeding territory has been established; (2) most landbird species are sedentary or migratory, not nomadic; and (3) most Australian passerines are long-lived, so surveys conducted within decadal timeframes may sample the same individuals. We examined the constancy of bird community composition by conducting repeat surveys at 29 sites in two vegetation types in the Namoi Valley, northern New South Wales, 7 years after the first survey. Bird assemblage composition in our study exhibited high levels of turnover between surveys, but 21 of 62 species present in both survey periods were significantly more likely to be found at the same sites in the second period as the first, and the tendency of most species was of site fidelity. Mantel tests demonstrated that assemblage composition at the same sites was more similar than expected by chance. Moderate levels of site fidelity among species and significant levels of assemblage composition constancy among sites should be the expectation when monitoring Australian landbird communities in wooded habitats over extended timeframes, except in the cases of major landscape transformation and extreme climatic disruptions.

**KEYWORDS**
agricultural landscape, biodiversity monitoring, bird movements, community composition, landscape fragmentation, site fidelity

## INTRODUCTION

Understanding long-term trends in biodiversity is essential to the conservation and management of biotic communities (Magurran et al., 2010), especially in highly fragmented ecosystems under intensifying pressure from climate change (Bennett et al., 2014; Mac Nally et al., 2009;

Matthews, 2021; Matthews et al., 2014). While dispersal and compositional variability in time and space fundamentally underpin biological diversity, some temporal trends represent a process of homogenization (McKinney & Lockwood, 1999; Szabo et al., 2011) or at least a deterministic loss of elements of biodiversity (Holmes & Sherry, 2001; MacHunter et al., 2006; Matthews et al., 2014; Sirami et al., 2009). These latter processes are antithetical to the goals of biological conservation and need to be fully understood if we are to stop biodiversity decline.

Australian bird communities are temporally dynamic with fluctuations in bird abundance in the arid zone ranging over at least an order of magnitude (Burbidge & Fuller, 2007; Reid et al., 1993). Woinarski and Tidemann (1991) documented threefold changes in avian abundance over 13 months in a deciduous savanna woodland (Top End, Northern Territory). In south-eastern Australia, a threefold increase in bird densities was recorded in woodland remnants over a 7-year interval (Maron et al., 2005) and twofold changes in avian density in consecutive years in woodlands and forests (Mac Nally, 1996; Recher et al., 1983).

However, some authors have preferred to emphasize the predictability of resource provision and its impact on avian life history strategies, even in arid Australia (Cody, 1994; Morton et al., 2011; Pavey & Nano, 2009). The sedentariness of many landbird species, especially small insectivores, is a global phenomenon (Kissling et al., 2012) and, in Australia, occurs in response to the persistent production of animal and plant food, despite the variable climate, particularly in microsites and better-watered parts of the landscape (Reid, 1999; Watson, 2011).

Bird community composition also varies spatially (beta diversity). Biogeographic patterns of bird distribution define and constrain the species pool in any one region (gamma diversity) and, within a region, distinct habitats influence local bird community composition in Australia (e.g. northern tropics: Woinarski et al., 1988; south-eastern forests and woodlands: Mac Nally, 1990; central Australian rangelands: Pavey & Nano, 2009) and elsewhere (Cody, 1985; Wiens, 1989). So, within distinct habitat types at local scales and in the absence of significant changes in land management (Sirami et al., 2009), extensive resource development (Carlin & Chalfoun, 2021), or major disturbances such as extensive wildfire (Tingley et al., 2016) or drought (Bennett et al., 2014; Weyland et al., 2019), what should be our expectation of bird community composition through time – constancy or change? Ford (1989) observed that this question merited detailed study.

Although temporal stability in bird community composition is reported in some ecosystems over a decade (Karp et al., 2011) or more (Machtans et al., 2014), long-term changes are more often reported, with the changes usually evident as an emergent property of all sites rather than at the individual site level. Maron et al. (2005) found a different dynamic in the subhumid Wimmera region of western Victoria after a 7-year interval by focussing on change at the site scale. They concluded that the 'change in distribution of most species did not differ significantly from that expected if species had redistributed at random' among sites (Maron et al., 2005: 383).

The conclusion of Maron et al. (2005) has obvious theoretical and practical importance. If this is generally the case, then a considerable amount of avian research and monitoring of bird communities worldwide might be less useful than researchers generally believe. Many of the conclusions from single-survey ('snapshot') studies of bird communities, and the inferences drawn from them, such as habitat preferences and patch-size requirements, may be questionable. For instance, in the earlier study of the Wimmera Buloke remnants, Watson et al. (2000) reported significant bird-habitat associations based on their site occurrence patterns. Similarly,

reserve selection processes could be suboptimal in highly fragmented, relictual landscapes were faunal turnover the norm (Felinks et al., 2011).

We argue that landbird communities in Australian wooded environments are generally relatively stable over annual periods, in the absence of major land-use change or landscape-scale disturbances (see Woinarski & Catterall, 2004, for an Australian example; also Renner & Bates, 2020). Our assertion is based on three well-supported propositions. First, landbird communities are dominated by passerine species which tend to remain faithful to a site once they have established a breeding home range following natal dispersal, whether as residents (Green & Cockburn, 2001) or migrants (Bell & Ford, 1987; Ford, 1998; Krebs, 2001: 61; van Dongen & Yocom, 2005). Second, adult Australian passerines are generally long-lived (Russell et al., 2004; Woinarski, 1985; Yom-Tov et al., 1992). Finally, most breeding species in Australian terrestrial bird communities are sedentary or migratory rather than nomadic (Cody, 1994; Maron et al., 2005; Pavey & Nano, 2009; Smith, 2015; Woinarski, 1985; Wyndham, 1978). These characteristics of Australian landbirds and their communities mean that repeat surveys after several years, in the absence of substantial habitat change, ought to result in similar lists of species to those first observed. We also argue that a snapshot can be a reliable method to obtain information about avian assemblages and their temporal and spatial dynamics. In support of our contentions, we present the results of a study in the Namoi catchment in north-west New South Wales with a similar temporal and analytical design to that of Maron et al. (2005). We argue that our results and conclusions should be expected when monitoring landbird communities in wooded environments within a localized region over extended periods of time. This expectation flows from what we term the 'same site similarity signal' (site self-similarity), which is a manifestation of the endpoint of spatial autocorrelation and the obverse of 'distance decay' in faunal similarity (Nekola & White, 1999; see also Sæther et al., 2013). We examine the extent to which habitat and regional differences may account for the relative constancy of composition in our study. Recommendations on ways to improve the design and analysis of studies of this type are given.

## METHODS

### Study region

The Namoi catchment drains west from the Great Dividing Range in northern NSW, Australia. The expansive floodplain associated with the Namoi River straddles the Brigalow Belt South and Darling Riverine Plains bioregions and is dominated by fertile black, grey, and brown vertosol soils favoured for dryland and irrigated cropping, and livestock (sheep and cattle) grazing. Two large nationally significant vegetation remnants (the Pilliga Scrub and Nandewar Range) flank the region, providing important habitat for a range of species (Date et al., 2002), while connectivity through the landscape is offered by the riparian corridor associated with the Namoi River and its tributaries and distributaries (Eco Logical Australia, 2009).

The distribution of native vegetation on the Namoi floodplain is correlated with flood frequency, and consists of two dominant associations, River Red Gum (*Eucalyptus camaldulensis*) riparian forests and woodlands with a shrub or grass understorey, and Coolibah (*E. coolabah*) woodlands grading into Black Box (*E. largiflorens*) woodlands, generally with a grass understorey, but often with varying cover of chenopod species away from the river in the west of the region.

We surveyed 29 sites across the Namoi floodplain (Figure 1), comprising 18 Coolibah ('Cool') and 11 River Red Gum ('RRG') sites. Another 27 sites in four other vegetation types were surveyed concurrently, and we analysed these additional data in the same way as described below (see Appendix S1: Tables S1–S3). The surveyed vegetation remnants were generally small (particularly in eastern and central areas), variously grazed by sheep or cattle or ungrazed, and many wooded sites had experienced some degree of historical vegetation thinning (ringbarking or timber collection).

## Climate

The study region has a semi-arid, subtropical climate with unreliable and sporadic rainfall (Figure 2). Mean annual rainfall declines from east to west across the region, varying from 592 mm near Boggabri (–30.7000°, 150.0333°; 246 m a.s.l.) to 436 mm near Walgett (–30.0167°, 148.1167°; 136 m a.s.l.), with a slight summer dominance (Bureau of Meteorology, www.bom.gov.au/climate/averages, accessed 1 May 2018). Mean maximum summer temperatures increase across the region from east to west, ranging between 32 and 35°C, while winter mean minima are 3–5°C.
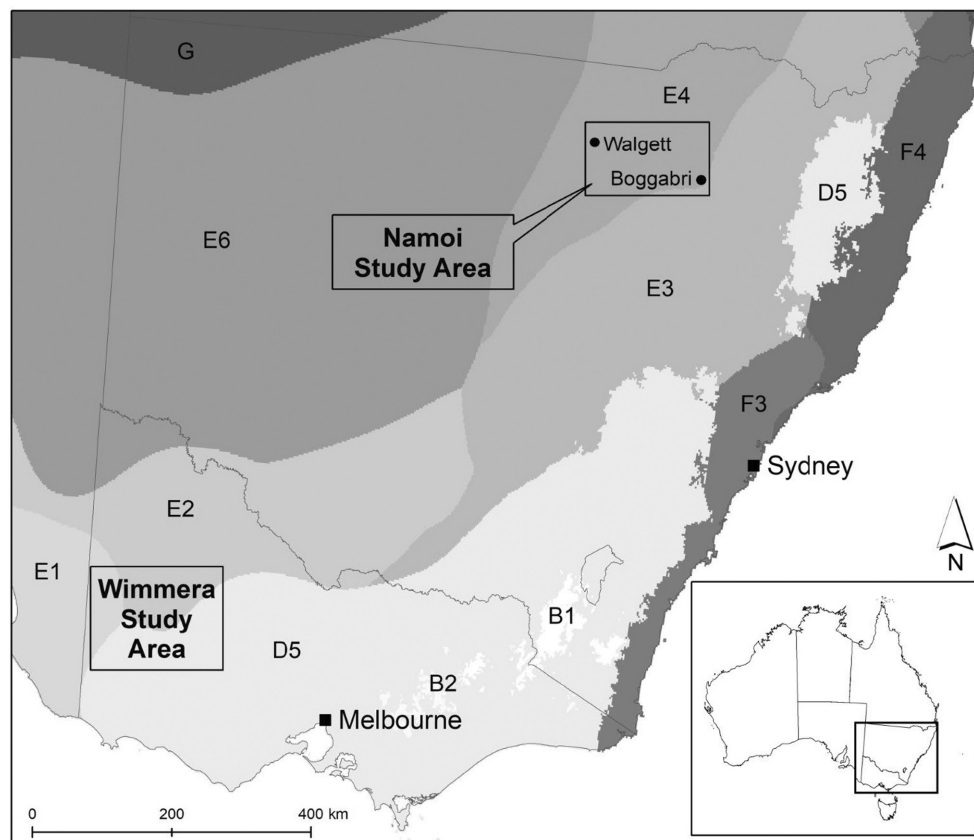


**FIGURE 1**  Our study region in the Namoi floodplain in northern NSW, and the study region of Maron et al. (2005) in western Victoria, showing the inter-relationships with agro-climatic zones (Hutchinson et al., 2005). Plant growth is limited by moisture across the Namoi study area, with the eastern half falling into agro-bioclimatic class E3 (Hutchinson et al., 2005), denoting a climate where most plant growth occurs in summer due to temperature limitation in winter, while the western half is in class E4 indicating relatively even plant growth throughout the year (i.e. mild winters). These categories align with the bioregional boundaries.
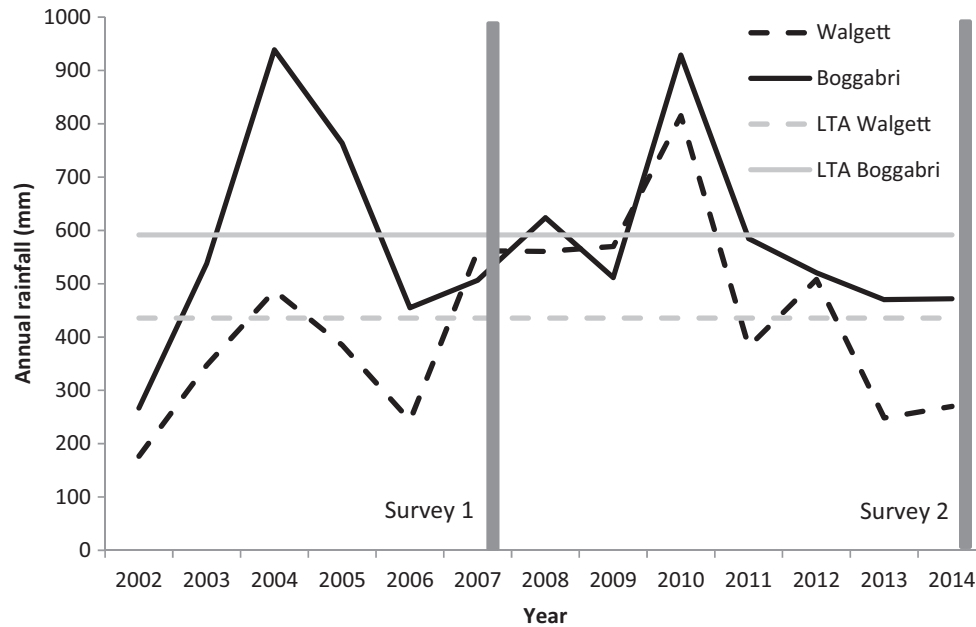
**FIGURE 2**  Yearly rainfall leading up to survey periods in 2007 and 2014, in relation to long-term averages (LTA) at Boggabri in the east and Walgett in the west of the region.

## Bird sampling methods

Birds were surveyed in a 2-ha area of the target vegetation type for 20 minutes during one morning (sunrise to 10:00) and one afternoon sampling period (16:00 to sunset) on different days between 10 September and 17 September 2007 (survey period 1). In 2014, birds were surveyed during two consecutive mornings (sunrise to 11:00) between 26 October and 9 November (survey period 2) in the same plots as those surveyed in 2007. Surveys were conducted by a single observer. Each of two observers surveyed the sites once within survey periods, and the identity of one observer was the same for the two survey periods. Weather conditions were noted and were generally fine and sunny (overcast on several mornings in 2007) and still or with a slight breeze during both survey periods. Very windy conditions and rain were avoided. All birds seen or heard in the 2-ha plot during surveys were recorded along with bird activity (e.g. flying through the plot, perched in a tree). Birds that were perched on the ground or foraging were regarded as 'in' the quadrat. Birds that flew through or over, or had no obvious interaction with the site (i.e. not hunting, feeding, nesting, etc.), were recorded as 'out' and excluded from further analysis so as to standardize survey area and focus on individuals and species reliant on the vegetation. Data were pooled over the two surveys within each survey period. Avian nomenclature follows Christidis and Boles (2008), and scientific names of birds are given in Appendix S1: Table S1.

## Analysis

We largely followed the analytical methods of Maron et al. (2005); details are provided where we departed from their approach. Table 5 provides a summary of species richness and abundance in the two study areas and the analyses used in both studies.

## Richness and abundance

Each species' abundance was tabulated at each site and across all sites. Wilcoxon signed-rank tests were used to compare abundances between the two survey periods for those species occurring in more than five sites in both survey periods. Pearson correlation analysis was used to determine whether log-transformed species richness and total density at sites were correlated across survey periods. A paired *t*-test of log-transformed total densities determined whether assemblage abundance differed between the two survey periods.

## Faunal turnover

Minimum turnover between survey periods (*T*) was calculated for each site for all species combined and for the three bird-movement categories – nomadic, migratory and sedentary – using the Jaccard Index of Dissimilarity (as used by Maron et al., 2005); 'minimum' turnover alludes to the unknown number of patch extinctions followed by colonization or colonization events followed by extinction between the two survey periods:

$$T = (C + E)^* \, 100 \, / \, S$$

where *C* is the number of observed colonization events; *E* is the number of observed extinction events, and *S* is the total number of species at a site in both periods.

Paired *t*-tests were performed between each pair of movement categories (after Maron et al., 2005). Assignment of species to movement categories followed Maron et al. (2005) with minor revisions (e.g. Chan, 2001; Reid & Fleming, 1992; Appendix S1: Table S1).

## Change in species distribution

For species that occurred in both periods, we calculated the percentage change in distribution (*D*) between the periods using the formula of Maron et al. (2005: Jaccard Index expressed as a percentage):

$$D = (C + E)^* \, 100 \, / \, N$$

where *N* is the total number of sites at which a species was observed in both periods. Pairwise comparisons of the change in distribution for each pair of movement categories were carried out using *t*-tests assuming unequal variances.

Monte Carlo randomization tests assessed whether the distribution of a species among sites in survey period 2 was consistent with a random reallocation from survey period 1 (1000 permutations used; our test statistic was the number of matching sites). Maron et al. (2005) used two-tailed tests, but we report both one-tailed and two-tailed tests given our alternative hypothesis. In addition to the randomization tests conducted by Maron et al. (2005), we used the discrete hypergeometric distribution to test if the number of sites occupied by a species in both periods, *k*, differed significantly from that expected by chance (Sokal & Rohlf, 1981). The discrete probabilities were calculated for each permissible value of *k*, given *K* (the number of sites occupied by the species in period 1), $n_2$ (number of sites occupied in period 2), and $N = 29$. Use of the hypergeometric distribution further allowed us to determine minimum sizes of *K*, *k*, and $n_2$, given *N*, for

which a species could have a significantly similar distribution among sites in periods 1 and 2. We restricted analyses to the 50 species which could return a significant result (i.e. in the upper 5% tail for a one-sided test). The probability mass function of the hypergeometric distribution is strongly asymmetric for small $N$, and so to ascertain the tendency of species to be more likely to occupy either a similar range of sites in survey period 2, or distinctly different sites, we evaluated how many species (of 62) fell in the upper 25th percentile, and lower 25th (22) and 50th (30) percentiles, respectively.

## Assemblage compositional change over time and structuring by habitat

Like Maron et al. (2005), Bray–Curtis similarity matrices were calculated for abundance and incidence (abundance converted to presence/absence) data sets, within and between surveys, with sites as the observations. The Bray-Curtis Index for incidence data is the Sørensen Index (SI), and it is directly interpretable in its similarity formulation as the proportion of species in common to two sites. Formally, it can be expressed as:

$$SI = 2a / (2a + b + c)$$

where $a$ is the number of shared species, and $b$ and $c$ are the number of species unique to each site.

The mean percentage similarity between each site in period 1 and all other sites in period 2, and the mean percentage similarity between sites within each survey period were calculated. We separately calculated the percentage similarity between the same sites across the two periods, to assess the relative strength of same-site similarity (Appendix S1: Figure S1). Analysis of similarity (ANOSIM, test statistic, $R_A$: Clarke, 1993) was used to explore differences between the bird assemblages recorded in each survey period, using both abundance and incidence data. Non-metric multi-dimensional scaling (NMDS) was used to ordinate sites (58 objects) according to bird community composition (70 species, having removed singleton occurrences) using the 'metaMDS' routine in 'vegan' (Oksanen et al., 2016) on the R platform (R Core Team, 2016). The influence of vegetation type and survey period on community composition in relation to the ordination was examined in vegan using multiple-axis correlation (routine 'envfit') and tested with 999 Monte Carlo randomizations. Bird abundance data were log-transformed ($\ln[x + 1]$) and ecological distance calculated using Bray–Curtis dissimilarity (Faith et al., 1987), where dissimilarity equals the complement of the similarity index.

### *Mantel tests*
We performed analyses not undertaken by Maron et al. (2005) to test whether the bird assemblages at sites in one period were more similar than expected by chance to the same sites in the other period. Mantel correlation tests (Mac Nally, 1990; Mantel, 1967), using the Pearson correlation coefficient, $R_M$, as the test statistic (Legendre & Fortin, 1989) were undertaken on the 2007 and 2014 Bray–Curtis distances using the log-transformed abundance and incidence data sets. Probabilities were evaluated using structured randomizations of the data, where the rows and columns of one matrix were jointly randomized (Goslee & Urban, 2007), accounting for the lack of independence of individual Bray–Curtis values. We extended this analysis by performing partial Mantel tests accounting for the effects of geographic distance between

sites to address the hypothesis that a significant similarity in assemblage composition at sites over time did not arise from the geographic distribution of the sites. Plots of Bray–Curtis assemblage distance versus geographic distance indicated a square-root transformation of the latter was required to linearize relationships (Goslee & Urban, 2007). Residuals from the regression of the 2007 and 2014 bird assemblage distances on the square root of geographic distances were correlated to obtain the partial correlation coefficient ($R_P$). A partial Mantel correlogram (Goslee & Urban, 2007) of the 2007–2014 assemblage correlations, using $R_P$ and separated into 12 distance classes, was examined to check for fine-scale spatial autocorrelation (Appendix S1: Figure S3). A second partial Mantel test controlled for the effects of habitat differences among sites, using a model triangular matrix representing the two habitats where cells representing sites of the same habitat took 0 and other contrasts took 1. All Mantel analyses, using 9999 randomizations for tests of significance, were conducted with 'ecodist' (Goslee & Urban, 2007, 2015) on the R platform (R Core Team, 2016).

## RESULTS

### Rainfall

In the 12 months preceding the 2007 survey, rainfall in the eastern (Boggabri) and western (Walgett) half of the study region was below the long-term average by 113 and 38 mm, respectively, while cumulative rainfall for the two preceding years was 6 mm above average in the east but 114 mm below average in the west (Figure 2). In the 12 months preceding the 2014 survey, rainfall was 133 and 199 mm below average in the east and west, respectively. This was the second dry year in a row in the region, with cumulative rainfall in the 2 years prior to the 2014 survey being 271 and 391 mm below average in Boggabri and Walgett, respectively.

### Richness and abundance

We recorded 86 landbird species across all sites and both surveys, 78 species in 2007 and 70 species in 2014 (62 shared). Mean species richness per site ($\pm 1$ SE) was similar in both survey periods ($13.6 \pm 1.07$ in 2007 and $12.7 \pm 0.92$ in 2014). Differences in species richness per site between years were not significant ($t_{28} = 1.33$, $p = 0.20$). Species richness across the 29 sites was positively correlated between the two periods ($R = 0.78$, $p < 0.001$). Although 14% more birds were observed in total in 2007 than 2014 (1913 individuals vs. 1641), bird density per site did not differ significantly between the two periods ($16.5 \pm 1.66$ vs. $14.1 \pm 1.45$ birds ha$^{-1}$; $t_{28} = 1.540$, $p = 0.13$). While 52 (60%) species were more abundant in 2007 versus 32 (37%) species in 2014, only seven species varied significantly in abundance between surveys: Galah, Cockatiel and Grey Shrike-thrush were more abundant in 2007 with Sacred Kingfisher, Noisy Friarbird, Pied Butcherbird and Willie Wagtail in greater abundance in 2014 (Table 1). All birds' abundance per site was correlated between the two periods ($R = 0.45$, $p < 0.05$, $n = 29$).

### Faunal turnover

Mean minimum species turnover per site was 63% (Table 2). Turnover of sedentary species (56%) was significantly lower than for migratory and

**TABLE 1** Species that changed significantly (Wilcoxon signed-rank test, $p < 0.05$) in abundance (mean density $\pm$ SE) in RRG/Cool sites between 2007 (survey period 1) and 2014 (survey period 2).

| | Abundance (individuals ha$^{-1}$) | |
| --- | --- | --- |
| Common name | 2007 | 2014 |
| Galah | $2.37 \pm 0.544$ | $1.35 \pm 0.265$ |
| Cockatiel | $0.41 \pm 0.106$ | $0.14 \pm 0.113$ |
| Sacred Kingfisher | $0.09 \pm 0.040$ | $0.28 \pm 0.084$ |
| Noisy Friarbird | $0.01 \pm 0.009$ | $0.07 \pm 0.030$ |
| Grey Shrike-thrush | $0.12 \pm 0.040$ | $0.06 \pm 0.027$ |
| Pied Butcherbird | $0.10 \pm 0.042$ | $0.26 \pm 0.067$ |
| Willie Wagtail | $0.22 \pm 0.073$ | $0.41 \pm 0.108$ |

**TABLE 2** (a) Mean minimum species turnover per site and mean percentage change in distribution per species in RRG/Cool sites ($n = 29$) for all species and for different mobility classes ($\pm$SE). Distributional change considers only those species that were recorded in at least one site during both survey periods. (b) Results of paired $t$-test comparisons of mean minimum species turnover and distributional change between bird movement categories.

| Category | Turnover (no. of sites) | Distributional change (no. of species) |
| --- | --- | --- |
| (a) | | |
| All species | $63 \pm 2\%$ (29) | $66 \pm 3\%$ (62) |
| Sedentary | $56 \pm 2\%$ (29) | $57 \pm 4\%$ (39) |
| Migratory | $79 \pm 5\%$ (24)[a] | $74 \pm 5\%$ (13) |
| Nomadic | $85 \pm 6\%$ (27)[b] | $87 \pm 5\%$ (10) |
| **Comparison** | **$t$-Value (df)** | |
| (b) | | |
| Sedentary vs. migratory | $4.309^{***}$ (23) | $2.305^{*}$ (24) |
| Sedentary vs. nomadic | $4.644^{***}$ (26) | $4.769^{***}$ (21) |
| Migratory vs. nomadic | 0.629 NS (22) | 1.915 NS (21) |

*Note*: Where the test is significant, the first-mentioned category had lower values of turnover and distributional change.

Abbreviation: NS, not significant.

[a]There were no migratory species recorded in either period at five sites.

[b]There were no nomadic species recorded in either period at two sites.

$^{*}p < 0.05$; $^{***}p < 0.001$.

nomadic species (82%; Table 2), which did not vary in turnover. Species turnover was lower in River Red Gum (60%) than Coolibah (64%) sites but not significantly so ($t_{25.14} = 0.95$, $p = 0.35$).

## Change in species distribution

For species that were recorded in both surveys, the mean difference in distribution between surveys among sites was 66% (Table 2). The mean difference in distribution was significantly greater for migratory and no-madic species with intermediate and high values of $D$, respectively, than for sedentary species with lower values of $D$ (mean = 57%; Table 2). The lower values of $D$ for migratory species (74%) was not significantly different from nomadic species (87%; Table 2). One species, Eastern Yellow Robin, had a $D$ of 0%, occurring in the same River Red Gum site in both years. A further 13 species – Rock Dove, White-bellied Sea-Eagle, Little Corella,

Sulphur-crested Cockatoo, Bluebonnet, Horsfield's Bronze-Cuckoo, White-throated Gerygone, Yellow Thornbill, White-plumed Honeyeater, Yellow-throated Miner, Noisy Friarbird, Grey-crowned Babbler and Black-faced Cuckoo-shrike – showed the maximum site fidelity possible given varying incidence in the two surveys. Little Corella was observed at four sites in 2014 and these sites had all been occupied in 2007, while the two and three sites occupied respectively by Black-faced Cuckoo-shrike and Yellow-throated Miner in 2014 had been occupied in 2007. Perhaps the most striking cases of site fidelity involved the Sulphur-crested Cockatoo (18 site occurrences in 2007, with 14 of these sites and no others occupied in 2014) and White-plumed Honeyeater (13 site occurrences in 2007, as a subset of the 14 occupied in 2014). In the nine remaining cases, the species was only detected at one site in either 2007 or 2014. Three species had very different incidence and distribution patterns in the two survey periods: Grey Fantail was detected at six sites in 2007 but none in 2014; Cockatiel was observed at 14 sites in 2007, three in 2014 and with only one site in common; Australian Raven was observed at 13 sites in 2007, 10 in 2014, with only four sites in common.

Two-tailed randomization tests showed that of the 46 species recorded at least twice in both surveys, 17 species occupied more of the same sites across survey periods than expected if their redistribution had been random (two-tailed test: Table 3), while the majority were distributed at random, either in or spanning the interquantile (95%) range. None occupied fewer same sites than expected by chance. Of the 17 species, 13 were sedentary (of 31 sedentary species), two of seven (Sacred Kingfisher and Little Friarbird) were migratory, and two of eight (White-browed Woodswallow and Black-faced Cuckoo-shrike) were nomadic species.

One-tailed tests using the upper 5% tail of the hypergeometric distribution revealed that 21 (42%) of 50 species exhibited significant site fidelity (Table 3). Of the 29 species randomly distributed across sites in the second survey compared with the first, 19 tended to occupy more of the same sites being in the upper 25th percentile of the hypergeometric distribution. Of the 30 species for which there were sufficient detections in both surveys to allow for the probability of redistribution among sites to fall in the lower 50th percentile, none had redistributed to that extent. The discrete probability of the distribution of five species with at least two occurrences in both surveys included the median, namely Cockatiel, Striated Pardalote and White-winged Triller (classified as nomadic), and the sedentary Laughing Kookaburra and Australian Raven. The remaining 41 species fell in the upper 50% of the distribution, with 33 species in the upper quartile (i.e. tending towards site fidelity; see Appendix S1: Figure S2d, Tree Martin, for an example).

## Assemblage compositional change over time and structuring by habitat

The composition of bird assemblages did not differ significantly between years, whether using abundance (ANOSIM, $R_A = 0.004$, $p = 0.342$) or presence/absence data ($R_A = 0.024$, $p = 0.146$). The average Bray–Curtis dissimilarity between survey periods was 80.7% using abundances; the within-group dissimilarities for survey periods 1 and 2 were 80.9% and 79.2%, respectively, whereas the mean dissimilarity in bird assemblages at each site between survey periods was 53.3%. Using incidence data, the mean dissimilarity between survey periods was 71.9%; within-group

**TABLE 3** Species whose observed distributional change ($D$, the test statistic) among sites was significantly less than expected ($p < 0.05$) on the basis of random redistribution between survey periods using 1000 Monte Carlo permutations (CI, confidence interval; two-tailed tests), and species occurrence in an improbably high number of the same sites in both surveys, based on the hypergeometric distribution (one-sided tests).

| | | Monte Carlo permutations | | | Frequency of occurrence in ($n = 29$ sites) | | | |
| | | Expected $D$ (%) | | | | | | |
| Species | Observed $D$ (%) | Mean | Lower (2.5%) CI | Upper (2.5%) CI | 2007 | 2014 | Same site both years | Hypergeometric test ($p$) |
|---|---|---|---|---|---|---|---|---|
| Sedentary | | | | | | | | |
| Peaceful Dove | 30 | 83 | 58 | 100 | 9 | 8 | 7 | ≤0.001 |
| Whistling Kite | 50 | 91 | 71 | 100 | 4 | 5 | 3 | ≤0.01 |
| Galah | – | – | – | – | 22 | 19 | 17 | ≤0.05 |
| Little Corella | 43 | 90 | 63 | 90 | 7 | 4 | 4 | ≤0.001 |
| Sulphur-crested Cockatoo | 22 | 62 | 48 | 77 | 18 | 14 | 14 | ≤0.001 |
| Red-rumped Parrot | 50 | 77 | 60 | 89 | 10 | 11 | 7 | ≤0.025 |
| Brown Treecreeper | 38 | 87 | 70 | 100 | 7 | 6 | 5 | ≤0.001 |
| Superb Fairy-wren | – | – | – | – | 4 | 7 | 3 | ≤0.05 |
| White-plumed Honeyeater | 7 | 69 | 50 | 83 | 13 | 14 | 13 | ≤0.001 |
| Noisy Miner | 29 | 67 | 47 | 79 | 15 | 14 | 12 | ≤0.001 |
| Yellow-throated Miner | 40 | 92 | 67 | 100 | 3 | 5 | 3 | ≤0.01 |
| Grey Shrike-thrush | 60 | 87 | 73 | 100 | 9 | 5 | 4 | ≤0.025 |
| Grey Butcherbird | 60 | 87 | 66 | 100 | 9 | 5 | 4 | ≤0.025 |
| Willie Wagtail | 43 | 77 | 63 | 90 | 9 | 13 | 8 | ≤0.01 |
| Restless Flycatcher | 50 | 91 | 71 | 100 | 5 | 4 | 3 | ≤0.01 |
| Magpie Lark | 47 | 71 | 56 | 87 | 13 | 13 | 9 | ≤0.025 |
| Eastern Yellow Robin | – | – | – | – | 1 | 1 | 1 | ≤0.05 |
| Migratory | | | | | | | | |
| Sacred Kingfisher | 58 | 84 | 69 | 100 | 6 | 11 | 5 | ≤0.025 |
| Little Friarbird | 38 | 70 | 56 | 87 | 13 | 13 | 10 | ≤0.01 |
| Nomadic | | | | | | | | |
| Black-faced Cuckoo-shrike | – | – | – | – | 2 | 6 | 2 | ≤0.05 |
| White-browed Woodswallow | 57 | 89 | 75 | 100 | 5 | 5 | 3 | ≤0.025 |

dissimilarities for survey periods 1 and 2 were 70.3% and 70.2%, respectively, with a mean dissimilarity between bird assemblages for each site across time of 46.6%. Clearly there is a strong within-sites to between-sites signal in the data sets, with lower same-site dissimilarity across time (47%–55%) than the dissimilarity among sites within and between survey periods (72%–79%).

Ordination in two dimensions showed that the pairs of sites sampled 7 years apart generally clustered close to each other and, while intermingled, River red gum bird assemblages tended to plot higher on axis 2 than Coolibah assemblages (Figure 3). Multiple axis-correlation tests confirmed these results: vegetation type was highly significant ($p = 0.001$), but the effect of survey period was not significant ($p = 0.833$), as with the ANOSIM results above. The one exception to the clustering of pairs of observations at each site involved a Coolibah site, labelled 'C12' in Figure 3; here, eight species were recorded in each survey period but only the Australian Magpie was common to both.
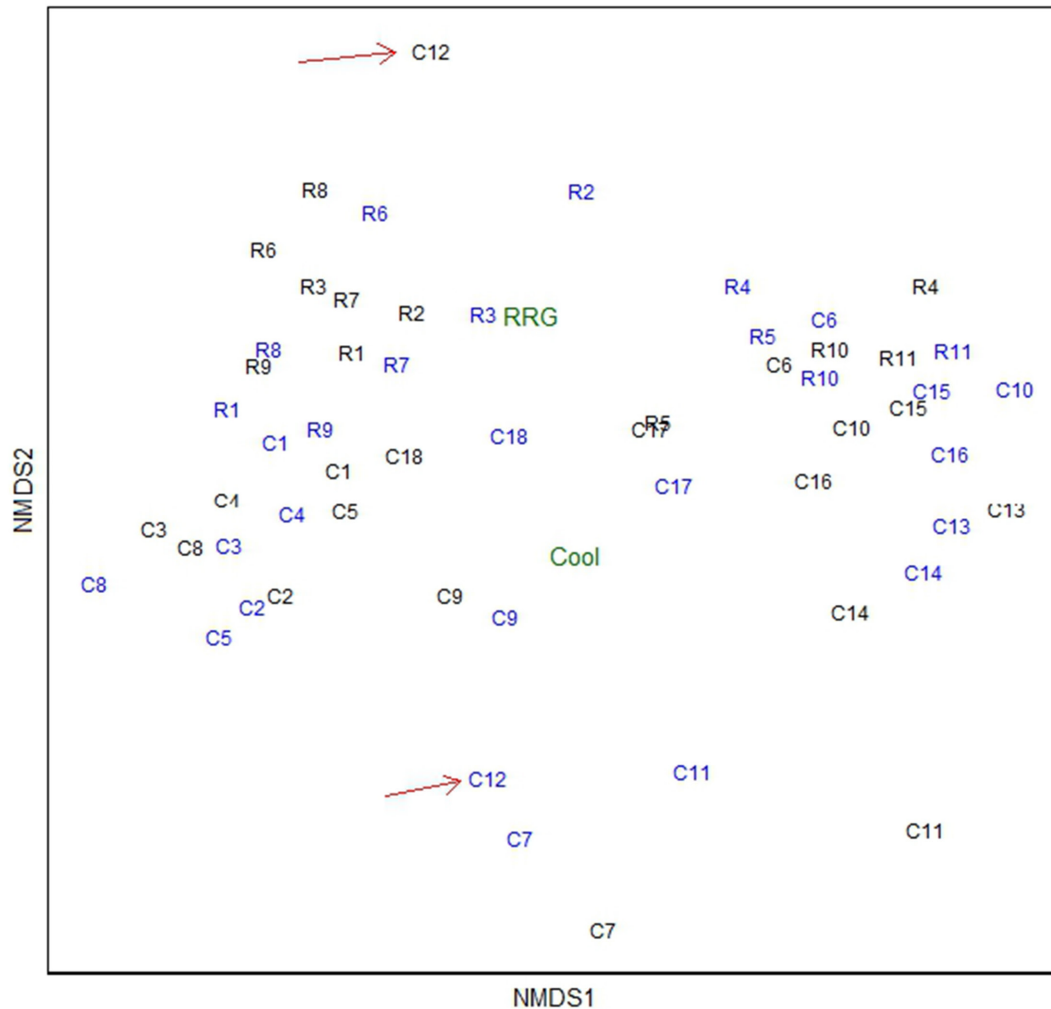
**FIGURE 3** Ordination of the 29 RRG/Cool sites in 2007 (black) and 2014 (blue), showing the habitat type of each site ('R' for River Red Gum, 'C' for Coolibah) and the habitat centroids. One site, 'C12' (red arrows), had a widely divergent assemblage composition between survey periods; otherwise, the self-similarity of sites is shown by their contiguity in multivariate space. Stress of two-dimensional solution = 0.17.

*Mantel tests*

Mantel tests of the correlation between the bird assemblages in 2007 and 2014 were highly significant for both bird abundance and species incidence (Table 4). Partial Mantel tests accounting for geographic distance between the sites were also highly significant, with $R_p > 0.49$ (both $p < 0.001$). The partial Mantel correlograms of the residuals showed no evidence of fine-scale spatial autocorrelation (i.e. residuals were not significantly positively correlated with distance over the first distance class). There was one significant negative lag at the third distance class in the incidence data set (Appendix S1: Figure S3) reflecting nonlinear fits in the 2014 assemblage – geographic distance relationships. Accounting for habitat differences among sites, partial Mantel correlations ($R_P > 0.56$) were highly significant (both $p < 0.001$; Table 4), indicating a high degree of site self-similarity in bird assemblage composition. Multiple regression models of distance matrices (after Goslee & Urban, 2007), fitting the 2007 observations in combination with geographic distance and habitat difference to the 2014 observations, were also highly significant (both $p < 0.001$; Appendix S1: Table S2).

**TABLE 4** Summary statistics for Mantel correlations ($R_M$) and partial Mantel correlations ($R_P$) comparing the bird assemblages in RRG/Cool sites ($n=29$) in 2007 and 2014, using Bray–Curtis dissimilarity matrices for species incidence and (log-transformed) abundance data, and Euclidean distance for habitat differences and the square root of the geographical distance between sites.

| | Mantel correlations |
|---|---|
| Mantel tests[a] | |
|     Incidence | $R_M = 0.564$*** |
|     Abundance | $R_M = 0.727$*** |
| Partial Mantel tests[b] | |
|     Incidence | |
|         Habitat | $R_p = 0.566$*** |
|         Distance between sites | $R_p = 0.492$*** |
|     Abundance | |
|         Habitat | $R_p = 0.727$*** |
|         Distance between sites | $R_p = 0.667$*** |

[a]Mantel correlations between 2007 and 2014 bird assemblage dissimilarity matrices.

[b]Partial Mantel correlations between the 2014 bird assemblage and the 2007 assemblage, controlling for the conditional variable.

***$p \leq 0.001$.

# DISCUSSION

In many respects, there were broad similarities across both studies, including the species composition of the two regions' avifaunas. Maron et al. (2005) did not provide a complete species list, but the earlier Wimmera study recorded 63 diurnal landbird species across all censuses (Watson et al., 2000, Table 3), and 43 of these (68%) were recorded in our study. The statistical similarities – high rates of turnover – between the two studies are discussed as well as the differences, namely the many (Namoi: 17–21 species, from a total of 86 species across both periods, at 29 sites) versus the few (Wimmera: five species, from a total of 76 species across both periods, at 26 sites) which showed significant site fidelity, and we provide explanations for these contrasting results. The strength of the Mantel and similar tests is highlighted before consideration of survey design and directions for future studies of this kind.

## Similarities and differences in results between the two studies

Species pools were broadly similar – both in identity and number – in the two regions – 76 species at 26 sites in the Wimmera, with 29% unique to either survey, compared with 86 species (28%) at 29 sites in the Namoi region. Bird communities at sites in our study were statistically similar in assemblage composition after a 7-year interval (Table 4). Maron et al. (2005) did not perform Mantel tests, but the Bray-Curtis dissimilarities given for both studies in Table 5, contrasting same-site values between survey periods with all between-survey values, are revealing. In both studies, mean between-period dissimilarity was high, particularly using abundance data – 77% in the Wimmera and 81% in the Namoi. However, the results diverged when comparing same-site dissimilarities – for abundance and incidence data respectively, Namoi sites were 27% and 35% more similar, compared with 4% and 8% at the Wimmera sites (Table 5). Another broad similarity between the two studies was the likelihood of finding roughly half the same

**TABLE 5** Comparison of statistical results between Maron et al. (2005) and the present study.

| Variable | | Maron et al. | | | This study | | |
| | | Buloke (26 sites) | | | RRG/cool (29 sites) | | |
| | | Time 1 | Time 2 | Outcome | 2007 | 2014 | Outcome |
|---|---|---|---|---|---|---|---|
| Species richness | Total overall | 76 spp. | | – | 86 spp. | | – |
| | Overall | 65 spp. | 65 spp. | – | 78 spp. | 70 spp. | – |
| | Site Mean±SE | 13.5±0.78 | 18.7±0.61 | Increase ($t_{25}=6.845***$) | 13.6±1.07 | 12.7±0.92 | No significant difference |
| | Outcome | No relationship between time periods ($r=0.13$ NS) | | | Significant relationship between periods ($r=0.78***$) | | |
| Species abundance | Overall | 1077 | 2942 | – | 1913 | 1641 | – |
| | Site Mean±SE | 4.6 | 12.6 | Significant increase | 16.5±1.66 | 14.1±1.45 | No significant difference |
| | Sig. increase | | | 16 spp. | | | 3 spp. |
| | Sig. decrease | | | 0 spp. | | | 4 spp. |
| Turnover ($T$) | All spp. Mean±SE | | | 63±2% | | | 63±2% |
| | Sedentary (S) Mean±SE | | | 57±3% | | | 56±2% |
| | Migratory (M) Mean±SE | | | 78±6% | | | 79±5% |
| | Nomadic (N) Mean±SE | | | 79±4% | | | 85±6% |
| | Outcome | | | S<N=M | | | S<N=M |

**TABLE 5**  (Continued)

| Variable | | | Maron et al. Buloke (26 sites) | | | This study RRG/cool (29 sites) | | |
|---|---|---|---|---|---|---|---|---|
| | | | Time 1 | Time 2 | Outcome | 2007 | 2014 | Outcome |
| Distribution change (D) | All spp. | Mean±SE | | | 68±4% | | | 66±3% |
| | Sedentary (S) | Mean±SE | | | 60±5% | | | 57±4% |
| | Migratory (M) | Mean±SE | | | 83±5% | | | 74±5% |
| | Nomadic (N) | Mean±SE | | | 81±6% | | | 87±5% |
| | Site faithful spp. | Randomization test | | | 5 spp. | | | 17 spp. |
| | | Hypergeometric test | | | – | | | 21 spp. |
| | Outcome | | | | S<N=M | | | S<N=M |

(Continues)

**TABLE 5** (Continued)

| Variable | | | Maron et al. Buloke (26 sites) | | | This study RRG/cool (29 sites) | | |
|---|---|---|---|---|---|---|---|---|
| | | | Time 1 | Time 2 | Outcome | 2007 | 2014 | Outcome |
| Assemblage composition | Abundance data | Between period, $BC_D$ | 76.9 | | ANOSIM | 80.7 | | ANOSIM/Mantel |
| | | Within period, $BC_D$ | 70.4 | 68.2 | Sig. diff. ($R_A = 0.298^{***}$) | 80.9 | 79.2 | A: No sig. diff. ($R_A = 0.004$) |
| | | Same site, $BC_D$ | 72.9 | | – | 53.3 | | M: Sig. correl. ($R_M = 0.727^{***}$) |
| | Pres/abs data | Between period, $BC_D$ | 59.7 | | ANOSIM | 71.9 | | ANOSIM/Mantel |
| | | Within period, $BC_D$ | – | – | No sig. diff. ($R_A = 0.066$) | 70.3 | 70.2 | A: No sig. diff. ($R_A = 0.024$) |
| | | Same site, $BC_D$ | 51.6 | | – | 46.6 | | M: Sig. correl. ($R_M = 0.564^{***}$) |
| Conclusion | | | Moderate same-site similarity (for pres/abs data only) | | | Moderate same-site similarity for both data sets | | |

*Note*: Statistical tests and test statistics are explained in Methods.

Abbreviations: –, not available; NS, not significant ($p > 0.05$).

$^{***}p \leq 0.001$.

species at a site in the second survey as the first. The mean Sørensen Index of Similarity (the complement of the Bray-Curtis dissimilarities on incidence data given in the bottom row in Table 5) was 48% for Wimmera sites and 53% in the Namoi valley, but despite these similar results, the number of species that were significantly more likely to occupy the same sites in both survey periods was greater in our study, namely 17, than the five reported by Maron et al. (2005) using the same randomization tests. The hypergeometric distribution and its probability mass function provided further evidence of self-site similarity and of the tendency for many species to occupy a similar range of sites in both survey periods. In our study, none of the 30 most frequently recorded species fell in the lower 50% quantile (tending towards a disparate pattern of site occupation in the two periods), whereas 40 of 62 species lay in the upper 25 percentile, indicating a tendency to reoccupy the same sites in the second period as the first. Of these, 18 of the 30 most frequent species did reoccupy a similar suite of sites ($p < 0.05$; one-tailed tests).

We reconcile these somewhat contradictory findings by providing a mechanical (numerical) explanation before considering the role of climate, particularly antecedent rainfall and drought, and other ecological mechanisms that could account for the differences, given the broad similarities in species pools and overall rates of turnover ($T$), Bray–Curtis dissimilarities and changes in distribution of species ($D$). Numerically, the divergent results are readily explained. The high turnover at the Wimmera sites arose largely from the almost threefold increase in abundance in the second survey with most species being more widely distributed across sites (Maron et al., 2005: 386–387). Significantly greater abundances and species richness across sites led to inflated values in all three measures of change, particularly the abundance-based Bray–Curtis dissimilarities. Consequently only a few species could have relatively stable abundances and site occupancy patterns between surveys. By contrast in our study, where neither abundance nor site richness varied significantly between surveys, and the variation in species richness among sites observed in the first year was highly correlated with the second (i.e. greater numerical stability), the comparably high levels of turnover and distributional change between surveys were caused by a longer tail of infrequently recorded species. Whereas 18 of 65 species (28%) occurred at a frequency of at least 33% site occupancy in the first round of Wimmera surveys (from data in Table 3 in Watson et al., 2000), only 14% and 19% of species were this frequent in the 2 years of survey in the Namoi region; data for the second round of Wimmera surveys by Maron et al. (2005) were not presented but the percentage must have been considerably greater than 28% given the much wider distribution of most species across sites and no extra species beyond those balancing the loss of species from the first survey. We assert that the longer tail of infrequent species found in our study, distributed sporadically across sites in either survey period, accounts for the high rates of turnover and distributional change common to both studies.

In terms of mechanistic explanations, the Wimmera sites were impacted by a large rainfall deficit in 1994 for the first round of surveys, and Maron et al. (2005: 389) concluded this probably contributed to the much greater abundances and expanded occupancy of sites by birds in the second survey; they speculated whether a change in state had been triggered by the 1994 drought from which a recovery was recorded during the later study. In contrast, the second survey period in our study was drier than the first, with a consequently smaller species pool and slightly lower site richness and abundance values (but not significantly so) than in the first surveys. Antecedent rainfall conditions would thus seem to be an important influence and account for some of the observed changes in abundance and species

distributions across sites. Observer differences in the Wimmera study may have contributed to some changes in recorded abundances, but were less likely to be influential in our study with one of the two observers involved in both survey periods. However, Maron et al. (2005) concluded observer discrepancies were probably minor. Survey design differences provide a third potential mechanism that may have caused a strong site self-similarity signal in our study – if there was greater habitat heterogeneity and ensuing high beta diversity among bird communities in different habitats, this could automatically generate high between-site to within-site variability. While the Wimmera study is described here and by Maron et al. (2005) as a study of bird communities in Buloke remnants, Watson et al. (2000) documented substantial floristic and structural variation among the sites, recognizing four classes of habitat, and with bird community composition varying significantly among habitat classes. Across the Namoi sites only in the second survey period did bird community composition vary significantly between River Red Gum and Coolibah sites: $R_A = 0.129$, $p = 0.035$; first period: $R_A = 0.029$, $p = 0.314$; cf. Watson et al. (2000, Table 5): $R_A = 0.156$, $p < 0.05$, for the Buloke sites in 1994/95), and so we conclude that the effect of a habitat-structuring contribution to species exhibiting strong site attachment ought to have been greater in the Wimmera study.

Potential ecological reasons for the major differences between the results of the two studies – the linked phenomena of (a) higher rates of compositional variability between-site and between-period compared to those within-site between-period, and (b) greater number of non-randomly distributed (i.e. site-faithful) species in our study than in Maron et al. (2005) – include the 'drought shock' (climate) hypothesis discussed above, the long-term stability of community composition in more productive and stable environments (such as our RRG/Cool sites, mostly in riparian zones), and an intrinsic tendency towards nomadism in Australian birds (as raised by Maron et al., 2005; see also Chan, 2001; Gibson et al., 2022). Given the majority of species was common to both studies, we rule out the third explanation except through a possible interaction with environmental gradients of productivity and stability. Maron et al. (2005), based on an observation by Watson et al. (2000), suggested another potential explanation for the high turnover they observed, namely that blended or ecotonal vegetation formations, like Buloke, should inherently have more compositionally unstable bird communities over time than those of single, well-defined vegetation formations (namely mallee and eucalypt woodland formations in the Wimmera). This hypothesis could be tested, in time, by expanding the range of sites in the Wimmera study area to include sites in these formations.

Support for a productivity basis to the contrasting results of the two studies can be found in our wider study of birds in six habitats (Appendix S1: Table S3). Abundance-based same-site dissimilarity at the non-RRG/Cool sites in the Namoi valley, i.e. in Black Box, Myall (*Acacia pendula*), revegetation and grassland habitats, averaged 76% (63% for incidence data), i.e. comparable to the results of Maron et al. (2005) in Buloke remnants. This result confirmed our expectation that the compositional stability of a site's bird community varies among habitats. Using abundances, River Red Gum sites in riparian environments had the most stable bird communities (49% abundance-based dissimilarity), followed by Coolibah (56%), while there was a large jump in turnover at Black Box (71%) and Myall and revegetation (73%) sites, rising to 83% turnover in grasslands. This pattern of greater compositional stability in wooded environments, especially in those with temporally more predictable resources (riparian and adjacent floodplains), driven at least in part by site-faithful sedentary birds, supports the proposition of Morton et al. (2011: 324) that increased, year-round reliability of resource production, under the control of water availability in

dry regions, should result in more resident bird species. At a larger scale, Nimmo et al. (2016) observed that bird communities in Victorian woodland environments were more stable over time (and during a drought) in landscapes with greater riparian area. Where the Buloke habitat sits on a resource-reliability gradient is unknown, but the turnover documented by Maron et al. (2005) was comparable to our result for Belah, both habitats being dominated structurally by long-lived confamilial trees.

The highly significant Mantel tests (Table 4), in conjunction with the similar species pools recorded in both periods, demonstrated a high degree of same site similarity in avifaunal composition from one survey period to the next. At the 29 RRG/Cool sites, a regression of distance matrices (2014 observations as a function of 2007 observations, habitat and geographic distances) accounted for 55% of the variance in the 2014 abundance dissimilarity matrix, with most variance explained by the observed distribution and abundance of species across sites in 2007 (see Appendix S1: Table S2 for details). As such, these results do not support the hypothesis of species generally redistributing themselves at random among sites, despite some doing so.

That we found many more species to be significantly site faithful using equivalent randomization tests – 17 of 62 species (Table 5), compared to five of 54 species in the Wimmera – is a major difference between the two studies. Nevertheless, for most species recorded in both survey periods, the null hypothesis that a species was randomly distributed among sites in period 2 compared with period 1 could not be rejected using the customary value of 0.05. A further similarity of the two studies was that Brown Treecreeper, Variegated Fairy-wren and Yellow Thornbill were significantly site faithful in both studies (Table 4); their other two site-faithful species were either not recorded in our study (Varied Sittella) or rarely (Spiny-cheeked Honeyeater). However, 10 species recorded during transect counts by Watson et al. (2000: Table 3) were found in our study to be site faithful, and so in this respect the differences outweigh the similarities. Further support for general site fidelity in our study was evidenced by 65% of 62 species recorded in both surveys lying in the upper quartiles of the hypergeometric distribution. Therefore, while we support the views of Maron et al. (2005) that there are high levels of compositional turnover at sites surveyed 7 years apart, our results emphasize the relative stability of assemblage composition, evidenced by the high level of site self-similarity due to many species being (or tending to be) site faithful.

## What factors drive stability and turnover in landbird communities?

Reviews of the Australian avifauna have noted that the proportion of nomadic species in bird communities increases in drier environments (Ford, 1989; Keast, 1959), as in any environment with irregular, seasonally unpredictable, pulses of resource production (Andersson, 1980). Like Maron et al. (2005), we found that sedentary species showed significantly lower levels of distributional turnover than migrant and nomadic species, and we anticipate that comparable studies of compositional change in arid regions ought to find lower levels of same-site similarity over time than we have reported. Counter to this expectation, Cody (1994) reported remarkably high levels of compositional predictability in 20 widely dispersed Mulga (*Acacia aneura*) bird communities in arid (and semi-arid) parts of Western Australia, Northern Territory and Queensland, compiled from single but lengthy site visits, with surveys conducted over a 9-year period (site self-similarity and temporal stability of the bird communities were not

explicitly addressed). Recher (2018) documented considerable change in assemblage composition and abundance from repeat surveys at four Mulga sites in Western Australia conducted 3 years apart under different climatic conditions, caused by an influx of nomadic species after flooding rains. Similarly, Maron et al. (2005) recorded almost three times the abundance of birds in their second survey as the first after earlier drought conditions had ameliorated, and we have concluded that the substantial increase in most species' incidence in the second survey accounted numerically for few species reoccupying a statistically similar range of sites. Neither in the Wimmera or Namoi studies did migrant and nomadic species differ significantly in the amount of distributional turnover, although there was a trend for nomadic species to exhibit greater turnover than migrants in our study, with the distributional change (D) across sites being 90% for nomads, 76% for migrants and 63% for residents (Table 5). One species we classified as nomadic that displayed significant site fidelity (White-browed Woodswallow, Table 3) has often been considered migratory in eastern Australia (Blakers et al., 1984; Higgins et al., 2006), and could be reclassified in future studies. Our results lend support to the notion that nomadic bird responses to changes in resource distribution, particularly those influenced by variable rainfall (Morton et al., 2011; Recher, 2018), contribute substantially to temporal turnover in assemblage composition. We agree with the view expressed by Maron et al. (2005) that current understanding of Australian bird movements is limited. We note the distinction between nomads that can undertake continental movements and those with a more limited range. For instance, McGoldrick and Mac Nally (1998) highlighted the sporadic occurrence of locally nomadic species (particularly nectarivores and frugivores) that track resource flows across Victorian woodland landscapes. Enhanced understanding of the scale of nomadic movements among species would allow scale-specific matching with climate drivers, allowing better interpretation of the factors contributing to compositional turnover between surveys. However, because nomadic bird species constitute a smaller proportion of assemblages than sedentary and migratory species in Australian woodlands dominated by long-lived trees, we consider site self-similarity, with a moderate proportion of species occupying a statistically similar range of sites, the general expectation in studies of this kind.

Much 'apparent turnover' (Lynch & Johnson, 1974) is caused by non-breeding birds that have been variously described as casual, locally nomadic, satellite, transient and vagrant (Ford, 1989; Hanski, 1982), that is, individuals passing through and stopping for a short time only, or which 'spill over' from adjacent habitats (Cody, 1994). Where the specific identity of these individuals differs from the sedentary and other breeding species, they will be a major source of variation in assemblages over time. Cody's (1994) characterization of species as 'core', 'peripheral' and 'casual' in Mulga habitats, or more simply 'core' and 'noncore' species (Matthews, 2021), has potential for making greater sense of studies like ours. Non-core species in the Namoi would include many in the long tail of infrequently recorded species – of 58 potential site occurrences across the two surveys, greater than 50% of species were recorded fewer than five times. As noted by Maron et al. (2005), studies of compositional stability should be restricted to the breeding season to eliminate some of the contribution to apparent turnover caused by transient or noncore species. Also if much compositional turnover – between successive surveys in one breeding season (days to weeks), between years, or over longer time frames (multi-annual) – can be apportioned to the transience ('churn') of non-breeding individuals and noncore species, then we assert that there should be an identifiable component of apparent turnover, which would then allow

'true turnover' to be estimated. True turnover could be defined as inter-annual change in site occupancy of breeding species. Further analysis of the Namoi data lends support to our concern that the perception of high turnover in assemblage composition might be partly or largely attributed to stochasticity around census techniques and sampling inefficiencies, including heterogeneous imperfect detectability among species (Boulinier et al., 1998; Kellner et al., 2018) and observer differences (Cunningham et al., 1999). The potential magnitude of this stochastic variation is given by the Bray-Curtis dissimilarities between each pair of censuses conducted in 2014 at our Namoi sites – mean dissimilarity, calculated on incidence data, between censuses was 46.5%, virtually identical to the corresponding value of the between survey period, same-site dissimilarity. Therefore, sampling stochasticity and low detection probabilities (due to large home-range size to sampling-area ratios) likely account for much of the apparent turnover between sites' assemblages over longer periods of time, and the amount of stochasticity will be inversely related to the adequacy of the census methods in terms of spatial scale and sampling intensity (Sæther et al., 2013).

The lack of significant differences in bird abundance and species richness between the two survey periods in our study was likely a consequence of the broadly similar rainfall patterns in the 1–2 years prior to the two surveys. This was fortuitous and should not be a general expectation. Even in studies with large changes in abundance as reported by Maron et al. (2005), we might have expected the same-site similarity signal to be evident with appropriate analyses such as Mantel tests. We argue that a detectable degree of site tenacity should be the norm for landbirds (particularly passerines) in most Australian habitats characterized by long-lived woody vegetation, while accepting that severe drought and other regional dynamics (see below) could overturn this expectation.

We have noted that survey design and sampling differences may have contributed to the contrasting outcomes of the two studies, but in this respect the greater stability of site occupancy found in our study was counter-intuitive. Aspects of the Maron et al. (2005) design that may have fostered greater turnover were the small quadrat size (1 ha) and the use of count data outside the breeding season. Our quadrat size (2 ha), while also small, will have resulted in more species being detected in individual counts, but our sampling frequency of two counts per survey period was low compared with nine counts in the Wimmera study. Ours was a true snapshot study in this respect, and restricted to the breeding season. Quadrat size needs to be considered in relation to typical home range and breeding territory sizes of the species comprising the regional avifauna, and in drier regions like the Wimmera and Namoi, home ranges might be considerably larger than 1–2 ha for most sedentary bird species (Paton et al., 2004, 2010; Reid, 1999). Nest location and daily foraging behaviour will then influence the likelihood of a sedentary species being detected when the sampling frame is small relative to territory size. Sampling issues – survey area, number and timing of repeat counts, and length of interval between survey periods – warrant further investigation, particularly in relation to home range size and the enumeration of transient or noncore species.

## High rates of compositional turnover in bird communities – Competing mechanisms and resulting patterns

We propose testable explanations for the contrasting findings of Maron et al. (2005) and our study in future studies of this type, and where any general random redistribution of sedentary species among sites, if observed,

cannot be attributed to major landscape change. Let us accept the premise that in highly fragmented landscapes, high rates of patch extinction occur in periods of drought (Bennett et al., 2014; Mac Nally et al., 2009; Reid, 1999; Watson, 2011). First, given the anticipated marked changes in occupancy patterns resulting from droughts, if recolonization events in the ensuing ameliorated conditions were at least partly random as is assumed by metapopulation theory (Hanski, 1982), then this could constitute a reset of the patch-occupancy distribution, which might then be relatively stable until another broad-scale perturbation. Second, and linked to the first through island biogeography theory, given the extreme relictual nature of the Wimmera study landscape – sites were located in small Buloke remnants mostly <20 ha in size, which were 'very isolated from other areas of native vegetation by cropping land' (Maron et al., 2005: 385) – it is possible the remnants are comparable to oceanic islands and subject to high rates of both local extinction and immigration (MacArthur & Wilson, 1967), explaining the essentially random re-assortment of bird assemblages across sites over 7 years. This hypothesis differs from the first (catastrophic drought) in predicting that patch composition will be found to be in a state of flux, and so the second explanation could be readily tested with further and more frequent surveys, as recommended by Bennett et al. (2024). Although not necessarily a random reorganization of species' distributions across sites, a third distinguishable pattern, one of systematic, long-term decline ('faunal relaxation'), is also likely in relictual landscapes, as has been documented for the avifauna of the Mount Lofty Ranges, South Australia (Paton et al., 2004; Prowse et al., 2021; Szabo et al., 2011). Studies of birds in native vegetation fragments in extensively cleared landscapes across southern Australia (Fraser et al., 2019; Lambeck, 1997; Mac Nally et al., 2002; Reid, 1999; Seddon et al., 2003; Szabo et al., 2011) and around the world (Blake & Karr, 1984; Matthews et al., 2014; Willson et al., 1994) have found identifiable subsets of species particularly susceptible to fragmentation. While few such studies have been long term, MacHunter et al. (2006) resurveyed 20 forest fragments in eastern Victoria 22 years after the initial surveys and found that rare species, defined by either low frequency of occurrence in patches in the earlier survey or low density, were more likely to have declined or disappeared in the second survey. Overall the patches had lost about nine species each, which the authors attributed to ongoing faunal relaxation. We would expect to see this third pattern in the extremely relictual Wimmera landscapes studied by Maron et al. (2005). As a counterfactual and according with our expectations, a fourth pattern of sedentary species' distributions among sites might be one of relative stability in successive years.

## Future research needs and recommendations

It is critical that more repeat surveys of the type considered here be documented to determine whether the results of Maron et al. (2005) are more general than we predict, and under what conditions they apply. There are several, continuing long-term woodland bird monitoring programs in southern Australia (e.g. Lindenmayer, 2022; Rayner et al., 2014; Szabo et al., 2011; reviewed by Bennett et al., 2024). Analyses of these data over multi-annual time steps should provide answers to some of the issues we raise. Controlling for beta diversity across study areas, as caused by habitat differences or biogeographical gradients, as we have shown using the matrix regression extensions to the Mantel tests, for multivariate responses (assemblage composition; Appendix S1: Table S2), will improve the confidence attached to conclusions in future studies. Furthermore, we

anticipate the use of generalized linear mixed models, specifying sites as a random effect, will allow the repeated-measures design of multi-annual surveys to be analysed with greater power and precision, when examining the responses of individual species. Terms for habitat, location (geographic gradients) and autocorrelation (spatial and serial), and use of appropriate link functions for binomial (or abundance) responses, will allow more sophisticated modelling of contingent distributions and partial effects (e.g. Lindenmayer et al., 2015).

We intend repeating the bird survey of the Namoi sites, and we recommend that the Wimmera sites be resurveyed. Repeat surveys in the latter region could determine whether comparable, near-random reassortment of species has again occurred in the intervening time, or if faunal relaxation (local extinctions structured by patch size and condition) has occurred, or whether assemblages were broadly and significantly similar at the site level to those observed previously. A distinction also needs to be made between breeding season censuses, typically spring – early summer in south-eastern Australia, and those conducted outside this period.

## CONCLUSION

Our data supported the contention that many sedentary bird species in the Namoi valley show a high degree of site-fidelity, owing to the prevalence of long-lived sedentary and (site-faithful) migratory species in the landbird avifauna of the region. While high levels of turnover in bird assemblage composition were exhibited, as reported by Maron et al. (2005), more than two-fifths of the species present in both survey periods in our study were significantly more likely to be found at the same sites in the second period as the first, and most species displayed a tendency in this direction given their position in the upper 25th percentile of the hypergeometric (probability mass function) distribution under the null model of random redistribution between survey periods. None of the 30 most frequent species with sufficient observations to allow discrete probabilities within the lower 50th percentile did so, whereas 18 of these, a majority, were significantly site faithful. Highly significant Mantel tests supported the contention that assemblage composition at the same sites was more similar after an interval of 7 years than expected under the alternate, random null hypothesis proposed by Maron et al. (2005).

The extreme relictual nature of the Maron et al. (2005) Wimmera landscape interacting with drought impacts potentially explains the difference in results between the two studies. The lower Namoi Valley contrasts with the Wimmera in retaining a higher degree of connectivity via riparian corridors and travelling stock routes and reserves, and this difference between the two regions may also have contributed to the contrasting results. Sampling stochasticity and low detection probabilities, as a result of small census area relative to home-range sizes and short census periods, should also be considered as part of future survey designs and when comparing results (Chandler et al., 2011; Tyre et al., 2003). High rates of faunal turnover among sites and distributional change among species were common to both studies, but were caused by different numerical processes, also worthy of future study. All things considered we believe that snapshot surveys can provide valuable insights into temporal and spatial dynamics of avian assemblages. They can also inform conservation land management. Sites with long-lived woody vegetation identified as having high conservation value at one time should, in the absence of catastrophic landscape change, have comparably high conservation status at a later time, provided land management and disturbance regimes remain similar.

## AUTHOR CONTRIBUTIONS

**Julian Reid:** Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Rhiannon Smith:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); writing – original draft (equal); writing – review and editing (equal). **Laura Scott:** Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Nick Reid:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); writing – original draft (equal); writing – review and editing (equal).

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## DATA AVAILABILITY STATEMENT

Data are available on request from the corresponding author, subject to permission from Cotton RDC & UNE.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.