

Reduced rainfall explains avian declines in an unfragmented landscape: incremental steps toward an empty forest?

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Abstract. Declines of formerly widespread bird species are being increasingly reported, with habitat loss, agricultural intensification and reduced rainfall frequently implicated. We report on temporal changes in the occurrence of birds over 21 years within continuous forest in the Warrumbungle Mountains to evaluate the influence of rainfall variability on changes in the abundance of birds and species occurrence. During this period, six common insectivores declined significantly (Superb Fairy-wren, *Malurus cyaneus*; White-throated Gerygone, *Gerygone albogularis*; Grey Shrike-thrush, *Colluricincla harmonica*; Rufous Whistler, *Pachycephala rufiventris*; Grey Fantail, *Rhipidura albiscapa*; Eastern Yellow Robin, *Eopsaltria australis*). Rainfall significantly predicted the abundance of 13 of the 25 most common species, with the rainfall period of both July–December of the previous year and the combined effects of six years of January–June rainfall correlated with changes in the abundance of birds. Prolonged drought has likely driven food shortages (especially of litter-dwelling arthropods), with changes in avian community composition reflecting changes in food availability. Thus, avian declines in southern Australia may reflect the combined effects of habitat fragmentation and other landscape-scale changes in concert with larger-scale ecological processes driven by decreased rainfall. Improved linkages between forested and agricultural landscapes at the regional scale are needed to buffer against local fluctuations in resources.

Additional keywords: agricultural landscape, drought, extinction debt, insectivore, local extinction, productivity.

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Introduction

In 1992, Redford cautioned that ‘we must not let a forest full of trees fool us into believing all is well’, and his ‘empty forest’ syndrome has since been applied to many more systems than the neotropical rainforests for which it was first described (Redford 1992). Seemingly intact habitats are increasingly found to lack the full complement of biodiversity and there is a growing realisation that setting aside large tracts of native ecosystems as the sole conservation strategy is insufficient (Karanth *et al.* 2010). Reduced abundances, retreating ranges and lower reproductive rates are all frequently reported, often manifesting in local or regional extinctions (Terborgh 1989). Declines in large-bodied mammals and birds (many of which occur at inherently low densities) in forest reserves were the original concern, but similar declines in common, widespread taxa, especially butterflies, birds and pelagic fish, are now known to occur (Gaston and Fuller 2008).

Some of the best examples of common, widespread species undergoing dramatic recent declines are of birds (Terborgh 1989; Ford *et al.* 2001; Gaston and Fuller 2007). These patterns have been described from all continents except Antarctica, with various forms of agriculture consistently implicated (Bennett and Watson 2011). The mechanisms driving these pervasive changes are not clear and are likely to vary between regions (Fuller *et al.*

1995). Extinction debt from past land clearing, disproportionate habitat loss on more productive soils, reduced food availability owing to eutrophication, agricultural intensification, effects of exotic predators and indigenous species becoming competitively dominant (miners (*Manorina* spp.) in south-eastern Australia, cowbirds (*Molothrus* spp.) in North America) have all been implicated, but no single process appears to hold generally (Donald *et al.* 2001; Watson 2011; Bennett and Watson 2011).

Changes in the frequency, variability and amount of rainfall interact with many of these processes, further diminishing overall availability of food resources, simplifying habitat structure and accentuating seasonal patterns of scarcity (Jetz *et al.* 2007). In a recent study of several forested landscapes in southern Australia, Mac Nally *et al.* (2009) showed that climatic factors can affect avian communities in intact, continuous habitats – elements of the landscape previously considered more resilient to the processes driving declines elsewhere. They suggested that reduced breeding success associated with reduction in available food may become more common as climatic variability increases. It is unclear, however, at what point these declines begin, whether some taxa are inherently more sensitive to nutritional shortages under reduced rainfall, the nature and scale of any time-lags, or whether these regional declines reflect population movements rather than local extinctions (Jetz *et al.* 2007).

Here, we use bird surveys conducted every year over 21 years to evaluate the effect of rainfall variation on the composition of avian communities. Compared with previous research on woodland birds, this study has three unique features: the study area is a large, intact reserve with minimal anthropogenic disturbance, so it is likely to represent the best-case scenario in terms of regional patterns of occurrence; all data were collected by a single observer, minimising issues associated with comparability and bias; and the data collection period spanned 21 uninterrupted years that coincided with one of the most severe and prolonged droughts recorded in Australia (2001–06 inclusive). Thus, this study provides a unique insight into how avian communities in intact systems change during a sequence of low rainfall years. In addition to describing declines and local extinctions, we explore the additive role of drought stress on fragmented populations, emphasising the complex trophic effects of alterations in rainfall.

Methods

Study area

Surveys were undertaken at three forested sites on private property in the Warrumbungle Mountains (31°17'S, 149°06'E; elevation 800 m above sea level (ASL)) ~25 km west of Coonabarabran, New South Wales, Australia, from January 1990 to December 2010. The vegetation of the study area is classed as forest (after Hnatiuk *et al.* 2003) or mixed open forest and woodland in older terminologies (e.g. Specht 1970). The forest is dominated by three tree species – Apple Box (*Eucalyptus bridgesiana*), Red Stringybark (*E. macrorhyncha*) and Inland Scribbly Gum (*E. rossii*) – with a canopy height of 18–22 m and crown cover of 10–30%; the understorey varies in extent, but is typically a diverse shrubby layer including Tableland Wattle (*Acacia caesiella*), *Cassinia quinquefaria*, Sticky Hop-bush (*Dodonaea viscosa*) and Sticky Daisy-bush (*Olearia elliptica*).

The forest had not been burnt for >50 years (see Postscript), and forest physiognomy did not change over the duration of the study. Although deep volcanic soils occur in the region, the soils of the study area are sandy loams. It is low-productivity forest, in contrast to the fertile, but largely cleared, agricultural land around Coonabarabran (altitude 500 m ASL). The surrounding region retains a significant proportion of native vegetation – ~44% remains native woodland and forest (Fig. 1). Apart from small clearings associated with homesteads and small farms (Fig. 1), the study site is continuous with the 23 000-ha Warrumbungle National Park and, further north, the 160 000-ha Pilliga State Forests and conservation zones. Combined, this contiguous forest comprises ~194 000 ha, or 83% of the woodland and forest within the study region (Fig. 1). There have been no changes in land-use over the duration of the study and, except for occasional feral Goats (*Capra hircus*), the forest is not grazed by exotic herbivores.

Surveys of birds were carried out within three 3.0-ha sites, each ~200 × 150 m. Two sites were next to each other, with the third 150 m away. The sites were near the edge of the forest bordering more sparsely wooded land, which had been cleared 30 years ago and is now regenerating naturally, and the edge of one site bordered cleared grazing land. The sites were all within 800 m of the property homestead and garden. The sites were originally delineated as part of the Australian Bird Count project organised by the Royal Australian Ornithologists' Union (now BirdLife Australia; <http://www.birdlife.org.au/>), and results from the first 5 years were submitted to this national project.

The observer walked an irregular traverse through each 3-ha study site for 20 min, recording all birds seen or heard within or flying over the site, then moving to the next site. The three sites were surveyed in the same order each time, and the route taken through each site was similar for each survey, counting only those individuals in front of the observer to minimise double counting. Surveys began at ~0830 hours and the three surveys were com-

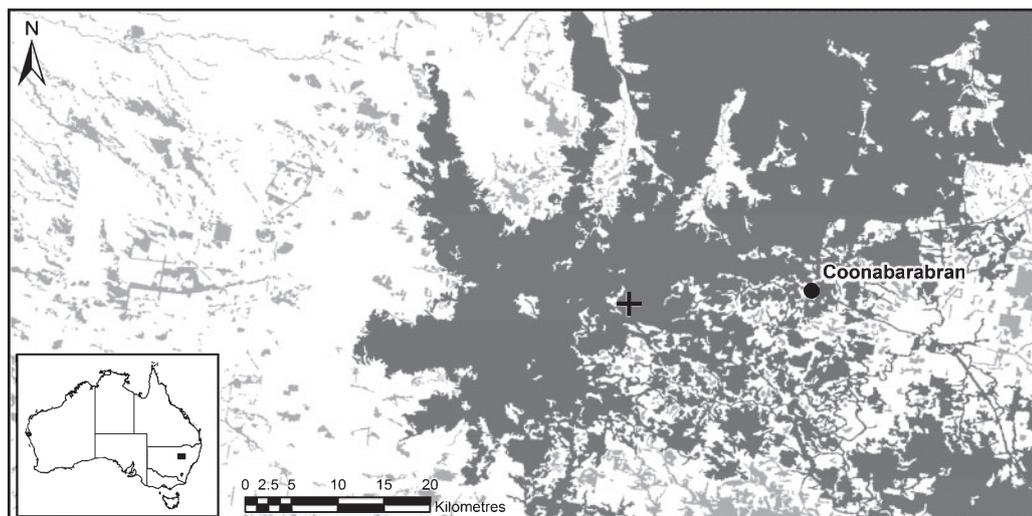


Fig. 1. The study area (marked with a cross) and the surrounding vegetation: native vegetation is shown by grey shading (44% of the area of the map), cleared land is unshaded. The Warrumbungle Mountains is the vegetated area to the west of the study area, and the Pilliga Forest is the large, irregular vegetated area to the north of Coonabarabran, which comprise a contiguous forest block of ~194 000 ha (dark grey). The edges of the figure are latitudes 31 and ~31.5°S and longitudes 148.5 to 149.5°E.

pleted in just over 1 h. Fixed-effort surveys with a sampling period of 60 min have been shown to be a suitable method for community-level studies of comparable sites (Watson 2004). All surveys were conducted by the same experienced surveyor. Over the 21 years of the study (1990–2010), we conducted 568 surveys, with an overall average of 27 surveys per year (range 6–48 surveys per year), equivalent to an average of 9 surveys for each 3-ha site per year or 0.75 surveys per month per site (see Supplementary material: Table S1). Although surveys were conducted in all months of the year over the study, not all months were surveyed annually; surveys were spread as evenly as possible in each year.

Rainfall 400 m from the study area was recorded in a rain gauge on a daily basis, yielding monthly and annual rainfall totals.

Analysis of avian abundance, density and reporting rates

Abundance (the number of individuals of each species summed over all surveys) was rescaled to a count per 100 surveys for all species detected in the study. For the most abundant species (>100 birds counted over the whole study period), scaled abundance was calculated for each year of the study and the result graphed. Pearson product-moment correlation coefficients (r) and coefficients of determination (R^2) were calculated and the slopes of the regression lines tested to detect any significant change to the abundance of a species over time ($P < 0.05$). In order to compare the densities of different species, average densities for the entire 21 years were calculated by dividing the summed abundance values for each species by the total number of surveys conducted $\times 3$ (each search area is 3 ha) to give an index of density (birds ha^{-1}). Although count data are generally considered to follow a Poisson distribution, we used linear regression for our analyses, as linear regression is a good approximation to the Poisson distribution for data with relatively high mean values. Where several predictors influence the count, linear regression is of more general application. The data were not suitable for analysis as time series because they were not collected in equally spaced time-intervals. However, the data were subjected to autocorrelation analysis to evaluate possible temporal autocorrelation, causing inflated values of R^2 (see below).

In addition to analysing individual species, we classified birds into seven feeding guilds – frugivores, granivores, generalists, nectarivores, insectivores, consumers of vertebrates and herbivores – using dietary information in Marchant and Higgins (1993), Higgins (1999), Higgins and Davies (1996), Higgins *et al.* (2001, 2006), Higgins and Peter (2002) and Radford and Bennett (2005). For each year of the study, the abundance of birds in each foraging guild was determined by summing the count of all members of that foraging guild over the year, scaled to 100 surveys. The data were graphed and tested by regression analysis to detect changes in abundance of each guild over the study period.

Reporting rates for each species and foraging guild were calculated as the percentage of surveys in which the species or guild was detected. Reporting rates are useful in helping define distributional ranges of species (Parsons *et al.* 2008), and tend to compensate for unequal search effort (Mac Nally *et al.* 2009). Reporting rates were calculated for each year of the study by

dividing the number of surveys in which a species was detected by the number of surveys conducted in that year. Pearson product-moment correlation coefficients (r) and coefficients of determination (R^2) were calculated for species and guilds and tested for significance as for analysis of abundance (above).

The abundance and reporting rates of birds over the 21 years of surveys provide time-series data, but are potentially influenced by the associated problems of temporal auto-correlation (i.e. the value of any observation may be correlated with observations nearby in time). Where significant correlations of bird abundance or reporting rate were found, standardised residuals were plotted against time to confirm whether the variance remained constant over time, the assumptions of normality were not violated and the pattern was not sinuous, indicating possible autocorrelation. A second test, the Durbin–Watson statistic d for first-order auto-correlation (Durbin and Watson 1950), was computed using the statistical package XLSTAT (Addinsoft: New York) and tested for significance using statistical tables of d .

Effect of rainfall

In the study area, rain falls throughout the year but with May and September the driest months. To discern any effects of rainfall on avian abundance, rainfall records for the study site were compared with abundances of individual species and foraging guilds over the 21 years of the study. Annual rainfall and different subsets of annual rainfall, for instance 5 months' rainfall in late spring–summer, 4 months' rainfall January–April and February–May, and 6 months' rainfall January–June and July–December were tested against individual species abundances. Rainfall for current years and 1, 2, 3, 4 and 5 years prior were examined separately and as running totals for any effect on bird abundances. The subdivisions of rainfall were similarly tested. Pearson product-moment correlation coefficients (r) and coefficients of determination (R^2) were calculated and the slopes of the regression lines used to infer significant relationships between rainfall and bird abundances. Owing to the large number of significance tests performed, the threshold level of significance was changed to a more conservative 0.01 (Bonferroni correction for multiple contrasts) rather than 0.05 used elsewhere in this paper.

We calculated the time-lag between various measures of rainfall and changes in abundance according to the following examples (with a full year = 1). For the previous year's July–December rainfall, the average lag time in years on the current year's abundance figures would be 0.25 years (midway through the 6 months July–December of the previous year) + 0.5 years (midway through the 12 months of the current year) = 0.75 years. For the cumulative January–June rainfall over the previous 5 years, the average lag time in years would be the mean of (0.75 + 1.75 + 2.75 + 3.75 + 4.75) + 0.5 (midway through the current year) = 3.25 years.

Results

Over the 21 years of the study, a total of 13 009 individuals of 84 species of bird was counted (Supplementary material: Table S1).

Bird abundances and reporting rates

The total count of individuals per survey declined by ~21% over the study, from an average of 25.1 birds survey⁻¹ in the 5 years

1990–94 to 19.8 birds survey⁻¹ in 2006–10 ($r=0.98$, $P=0.021$). The number of species observed each year over the 21 years of surveys increased from an average of 40.8 species year⁻¹ in the 5 years 1990–94 to 46.6 species year⁻¹ in 2006–10 ($r=0.66$, $P=0.34$).

The 84 species observed, their densities, abundances and reporting rates are listed in the Supplementary material (Table S2). The most abundant species were not necessarily those with the highest reporting rates: the Yellow-faced Honeyeater (*Lichenostomus chrysops*) was the most abundant species, but had a lower reporting rate (70.6%) than the White-throated Treecreeper (*Cormobates leucophaea*) (75.8%), whereas White-winged Choughs (*Corcorax melanorhamphos*) ranked higher on the scale of abundance (13th) than on reporting rate (24th), a result of this species usually occurring in large groups (Table S2). Four species were detected in $\geq 50\%$ of surveys: the White-throated Treecreeper, Yellow-faced Honeyeater, Spotted Pardalote (*Pardalotus punctatus*) and Grey Fantail (*Rhipidura albiscapa*).

The 25 most numerous species, with more than 100 individuals recorded over the 21-year study period (i.e. approximately one or more individuals per five surveys), were subjected to year-by-year analysis of reporting rate and abundance. Those species

showing significant declines were all small insectivores: the White-throated Gerygone (*Gerygone albogularis*), Superb Fairy-wren (*Malurus cyaneus*), Rufous Whistler (*Pachycephala rufiventris*), Grey Shrike-thrush (*Colluricincla harmonica*), Grey Fantail and Eastern Yellow Robin (*Eopsaltria australis*). None of these species showed evidence of temporal auto-correlation except for the Eastern Yellow Robin (d statistic 0.93 for abundance, 0.55 for reporting rate; Table 1). Nevertheless, the results for Eastern Yellow Robin were highly significant ($P=0.008$ for both abundance and reporting rate), and the declines in these two parameters were considered to be true declines.

Two other small insectivores, the Weebill (*Smicrornis brevirostris*) and Spotted Pardalote, and two honeyeaters, the Eastern Spinebill (*Acanthorhynchus tenuirostris*) and Red Wattlebird (*Acanthochaera carunculata*), increased in abundance and reporting rate over the study period, with the Weebill trends showing evidence of temporal auto-correlation ($d=1.06$ for abundance, 1.08 for reporting rate; Table 1). The observed increases in abundance and reporting rate for Weebills were highly significant ($P=0.0001$ and 0.001) and the increases in these two parameters were considered to be true increases. The abundance and reporting rate of several other small insectivores (White-throated Treecreeper, Striated Pardalote (*Pardalotus*

Table 1. Abundance and reporting rates of the 25 most abundant species of birds recorded in the study, divided into those showing a significant decline, increase or no change over the period of the study

Where a significant change was detected ($P < 0.05$), the Durbin–Watson d statistic to detect temporal auto-correlation was computed. The probability (P) that the species is declining or increasing (slope of line significantly different from 0) or showing no change (slope of line not significantly different from 0) is shown as a P value. For the value of the Durbin–Watson statistic (d), if $< 5\%$ significance point (1.221) for $n=21$ and one regressor, there is evidence of temporal auto-correlation

		Abundance	P	d	Reporting rate	P	d
Declining species							
White-throated Gerygone	<i>Gerygone albogularis</i>	Decline	0.044	1.93	No change	0.42	
Rufous Whistler	<i>Pachycephala rufiventris</i>	Decline	0.002	2.65	No change	0.26	
Grey Shrike-thrush	<i>Colluricincla harmonica</i>	Decline	0.006	1.43	Decline	0.027	1.61
Grey Fantail	<i>Rhipidura albiscapa</i>	Decline	0.0007	1.45	Decline	0.016	1.29
Eastern Yellow Robin	<i>Eopsaltria australis</i>	Decline	0.008	0.93	Decline	0.008	0.55
Superb Fairy-wren	<i>Malurus cyaneus</i>	No change	0.15		Decline	0.019	1.39
No significant change							
Crimson Rosella	<i>Platycercus elegans</i>	No change	0.10		No change	0.71	
Laughing Kookaburra	<i>Dacelo novaeguineae</i>	No change	0.45		No change	0.21	
White-throated Treecreeper	<i>Cormobates leucophaea</i>	No change	0.33		No change	0.56	
Striated Thornbill	<i>Acanthiza lineata</i>	No change	0.11		No change	0.052	
Buff-rumped Thornbill	<i>Acanthiza reguloides</i>	No change	0.74		No change	0.99	
Striated Pardalote	<i>Pardalotus striatus</i>	No change	0.66		No change	0.14	
Yellow-faced Honeyeater	<i>Lichenostomus chrysops</i>	No change	0.10		No change	0.13	
White-eared Honeyeater	<i>Lichenostomus leucotis</i>	No change	0.71		No change	0.84	
White-plumed Honeyeater	<i>Lichenostomus penicillatus</i>	No change	0.28		No change	0.15	
White-naped Honeyeater	<i>Melithreptus lunatus</i>	No change	0.18		No change	0.051	
Noisy Friarbird	<i>Philemon corniculatus</i>	No change	0.36		No change	0.25	
Pied Currawong	<i>Strepera graculina</i>	No change	0.41		No change	0.10	
Leadon Flycatcher	<i>Myiagra rubecula</i>	No change	0.20		No change	0.18	
White-winged Chough	<i>Corcorax melanorhamphos</i>	No change	0.86		No change	0.82	
Silvereye	<i>Zosterops lateralis</i>	No change	0.69		No change	0.91	
Increasing species							
Weebill	<i>Smicrornis brevirostris</i>	Increase	0.0001	1.06	Increase	0.001	1.08
Spotted Pardalote	<i>Pardalotus punctatus</i>	Increase	0.017	2.48	Increase	0.004	2.57
Eastern Spinebill	<i>Acanthorhynchus tenuirostris</i>	Increase	0.036	1.96	Increase	0.005	1.74
Red Wattlebird	<i>Acanthochaera carunculata</i>	Increase	0.005	1.82	Increase	0.001	1.87

striatus), Striated Thornbill (*Acanthiza lineata*), Buff-rumped Thornbill (*A.reguloides*), and Leaden Flycatcher (*Myiagra rubecula*)), honeyeaters, a consumer of vertebrates (Laughing Kookaburra (*Dacelo novaeguineae*)), a large insectivore (White-winged Chough) and a generalist (Pied Currawong (*Strepera graculina*)) remained relatively unchanged over the study (Table 1). Although not in the top 25 most-abundant species, the Noisy Miner (*Manorina melanocephala*; 48th in the list based on abundance) showed a sharp increase in reporting rate and abundance after 2000, when they established a colony near the study site. The species was first recorded in the study area in May 2000, and was recorded sporadically in seven subsequent surveys, the last in June 2010 (a total of 26 birds recorded in 315 surveys in that period).

There was no significant change in either abundance or reporting rate for any of the seven guilds over the study period. All of the declining species were small insectivores, and two other small insectivores – Weebill and Spotted Pardalote – increased. Based on fundamental differences in diet (both of the species that increased are psyllid specialists (Higgins and Peter 2002)), we removed these two species and re-examined trends in the insectivore guild (Fig. 2), which revealed a significant decrease in

abundance ($P=0.0002$) and reporting rate ($P=0.006$) for insectivores. We further subdivided insectivores into those that foraged wholly or mainly on the ground, and those that foraged wholly or substantially on other substrates, including leaves, bark, branches and aerially. Ground-foragers showed significant declines in abundance ($P=0.002$) and reporting rate ($P=0.0008$) whereas the above-ground foragers did not. Including Weebills and Spotted Pardalotes in the above-ground-foragers, there was little change in abundance or reporting rate in this foraging guild over the years. When these two species were excluded, above-ground feeders declined significantly in abundance ($P=0.001$) but not significantly in reporting rate ($P=0.081$; Table 2).

Effect of rainfall

Annual totals and a 2-year moving average of rainfall in the study area from 1989 to 2010 were calculated (Fig. 3), with an emphasis on the period of drought from 2001 to 2006, and annual rainfall returning to the long-term average in 2007. Rainfall had a significant correlation with the abundance of 13 of the 25 most abundant species of birds (Table 3). Ten of these

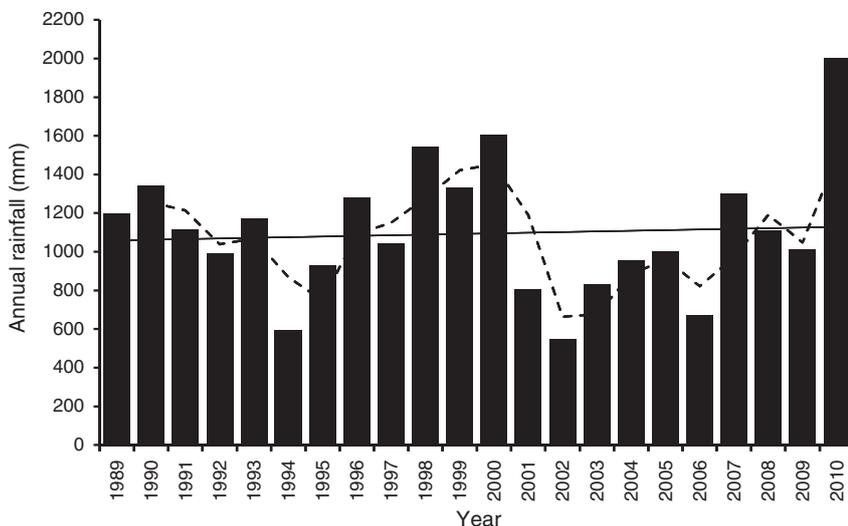


Fig. 2. Annual rainfall at the study site (1990–2010) showing trendline (solid line) and 2-year moving average (dotted line). The 6-year rainfall deficit from 2001 to 2006 inclusive is evident.

Table 2. Changes in abundance and reporting rate of insectivores over the 21 years of surveys

Abundance and reporting rate are examined for all insectivores, insectivores excluding two specialist foragers (Weebill and Spotted Pardalote), ground-foraging insectivores, and above-ground foragers (all and excluding Weebill and Spotted Pardalote); for guild into which species classed, see Supplementary material Table S2. Where a significant change was detected ($P < 0.05$), the Durbin–Watson d statistic to detect temporal auto-correlation was computed. The probability (P) that the group is declining or increasing (slope of line significantly different from 0) or showing no change (slope of line not significantly different from 0) is shown as a P value. For the value of the Durbin–Watson statistic (d), if $<5\%$ significance point (1.221) for $n = 21$ and one regressor, there is evidence of temporal auto-correlation

Group	Abundance	P	d	Reporting rate	P	d
All insectivores	No change	0.12		No change	0.06	
Insectivores excluding Weebill + Spotted Pardalote	Significant decline	0.0002	1.78	Significant decline	0.006	1.75
Ground-feeders	Significant decline	0.002	1.43	Significant decline	0.0008	1.64
Above-ground-feeders including Weebill + Spotted Pardalote	No change	0.51		No change	0.75	
Above-ground-feeders excluding Weebill + Spotted Pardalote	Significant decline	0.001	1.85	Non-significant decline	0.081	

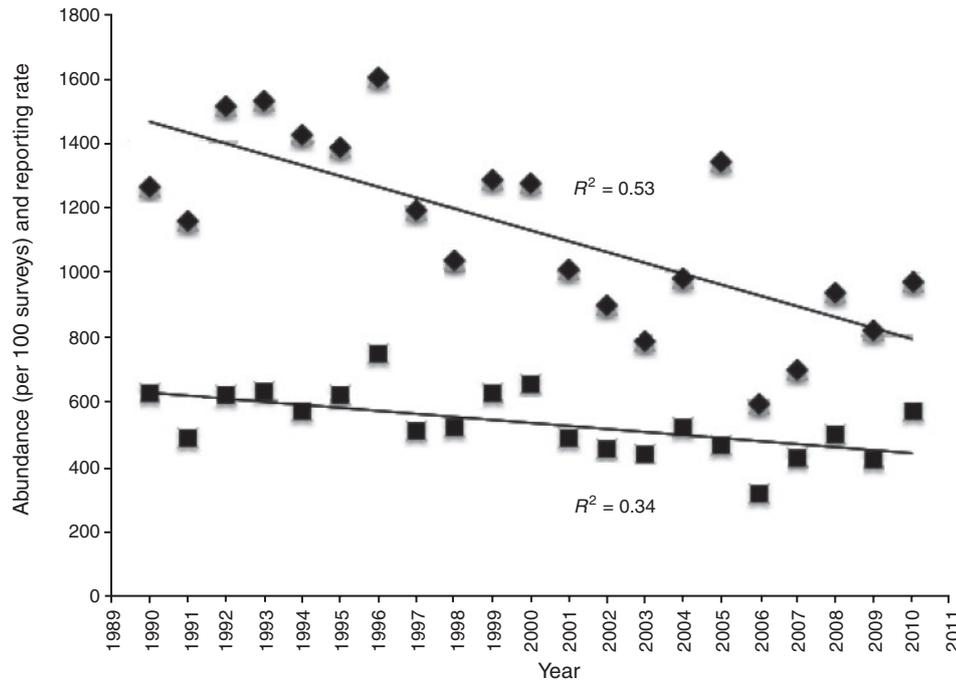


Fig. 3. Annual abundance (diamonds; number per 100 surveys) and reporting rate (squares) of all insectivores combined excluding Weebills and Spotted Pardalotes (1989–2010) with fitted regression lines.

relationships were positive (i.e. increased rainfall correlated with increased abundances) and three (Red Wattlebird, Crimson Rosella (*Platycercus elegans*) and Pied Currawong) were negative (i.e. increased rainfall correlated with decreased abundances) (Table 3). The time-lag for these effects varied from 0.75 years for species such as the Yellow-faced Honeyeater and Eastern Spinebill to 1.25–1.75 years for most insectivores and even longer periods for a generalist (Pied Currawong; Fig. 4).

Further analysis was carried out to see if rainfall at particular times of year had an effect on the abundance of individual species. The only subsets that yielded significant results were the half-yearly divisions of January–June and July–December. The average July–December rainfall at the study site for the past 21 years (mean \pm s.e. 585.7 \pm 55.9 mm) was 16% greater than the January–June rainfall (503.9 \pm 33.9 mm). Over the 21 years of the study, annual January–June or July–December rainfall did not decline significantly based on single-year figures, but when the rainfall of the present and past 5 years (i.e. 6-year running totals), was plotted against the current year, only January–June rainfall was found to decline significantly ($R^2 = 0.391$, 18 d.f., $P = 0.002$), the other two indices remaining relatively constant ($P > 0.10$ for both).

The abundance of three species of honeyeater, and the nectarivore guild, increased significantly in response to increased July–December rainfall of the previous 1 or 2 years. However, for six insectivorous species, and for the ground-feeding insectivore guild, higher rainfall in January–June was associated with greater abundance of birds, with various combinations of the present and previous 1, 2, 3, 4 and 5 years being important for these species (Table 3).

Discussion

Declines of woodland birds

Our findings relate to a largely intact, unfragmented landscape, until now considered to act as one of the principal refugia or source populations for many woodland-dependent species in the region. In our study, we found that the abundance or reporting rate, or both, of six small insectivores declined significantly over two decades, and that all six that declined were among the 20 most abundant species recorded in our study. These were not rare species becoming rarer but common species recorded at high densities becoming dramatically less abundant over time. Two species, the Grey Fantail (density 0.42 birds ha⁻¹) and Grey Shrike-thrush (0.23 birds ha⁻¹) are noteworthy because they are not on the list of 26 ‘declining woodland birds’ (Watson 2011) but share many ecological attributes with them (resident and insectivorous; primarily small-bodied and ground-foraging), suggesting the group of ‘declining woodland birds’ may not be as exclusive as was once hoped.

We also found that insectivores as a group showed significant declines in abundance and reporting rate once the influence of two specialised foliage gleaners was removed. Ground-foraging insectivores appeared to be particularly susceptible to declines, consistent with results from previous studies (Reid 1999; Bennett and Watson 2011). An additional group of insectivores (including the Restless Flycatcher (*Myiagra inquieta*), Speckled Warbler (*Chthonicola sagittata*), Inland Thornbill (*Acanthiza apicalis*) and Chestnut-rumped Heathwren (*Hylacola pyrrhopygia*)) can be considered ecologically extinct, occurring at densities < 2 birds 100 ha⁻¹, below the threshold at which they may be considered to ‘interact significantly with other species’ (Estes

Table 3. Relationship between rainfall and abundances of the 25 most abundant bird species (positive or negative), showing the maximum value for the coefficient of determination (R^2) and its probability (threshold level $P=0.01$), the effective rainfall period and the time-lag

Guild and species	Relationship	Maximum R^2	P	Effective rainfall period	Time-lag
Nectarivores					
All nectarivores	Positive	0.408	0.002	Jul–Dec	Previous year
Yellow-faced Honeyeater	Positive	0.441	0.001	Jul–Dec	Previous year
White-eared Honeyeater	Positive	0.500	0.0003	Jul–Dec	2 years previous
Noisy Friarbird	Negative	0.210	0.037	Jul–Dec	2 years previous
White-naped Honeyeater	Positive	0.095	0.17	Whole period	Previous 18 months
White-plumed Honeyeater	Positive	0.138	0.097	Jul–Dec	Previous year
Eastern Spinebill	Positive	0.348	0.005	Jul–Dec	Previous year
Red Wattlebird	Negative	0.366	0.004	Jan–Jun	Previous 3 years
Insectivores					
All insectivores		0.109	0.14		
All ground-feeding insectivores	Positive	0.364	0.004	Jan–Jun	Present + previous 1, 2, 3, 4 and 5 years
All above-ground-feeding insectivores	Negative	0.231	0.027	Jul–Dec	3 years previous
Spotted Pardalote	Negative	0.235	0.026	Jan–Jun	Present + previous 1, 2, 3 and 4 years
Striated Pardalote		0.105	0.15		
Grey Fantail	Positive	0.304	0.010	Jan–Jun	Present + previous 1, 2, 3 and 4 years
White-throated Treecreeper	Positive	0.368	0.004	Jan–Jun	Previous 1, 2 and 3 years
Rufous Whistler	Positive	0.243	0.023	Jan–Jun	Present + previous 1, 2, 3, 4 and 5 years
Striated Thornbill	Positive	0.303	0.010	Jan–Jun	Previous year
Buff-rumped Thornbill		0.158	0.074		
Grey Shrike-thrush	Positive	0.703	0.000002	Jan–Jun	Present + previous 1, 2, 3, 4 and 5 years
White-winged Chough	Positive	0.308	0.009	Jul–Dec	3 years previous
White-throated Gerygone	Positive	0.329	0.007	Jan–Jun	Present + previous 1, 2, 3, 4 and 5 years
Superb Fairy-wren		0.034	0.42		
Eastern Yellow Robin		0.071	0.24		
Leaden Flycatcher	Positive	0.279	0.014	Jan–Jun	Present + previous 1, 2, 3, 4 and 5 years
Weebill	Negative	0.220	0.032	Jan–Jun	Present + previous 1, 2, 3, 4 and 5 years
Granivores					
All granivores		0.089	0.19		
Crimson Rosella	Negative	0.315	0.008	Jul–Dec	2 years previous
Generalists					
All generalists	Negative	0.200	0.042	Whole period	Previous 5 years
Pied Currawong	Negative	0.323	0.007	Jul–Dec	4 years previous
Vertebrate-consumers					
All vertebrate-consumers	Negative	0.165	0.068	Whole period	Previous 30 months
Laughing Kookaburra	Positive	0.196	0.044	Jan–Jun	Previous 1, 2, 3, 4 and 5 years
Frugivores					
All frugivores	Positive	0.407	0.0009	Whole period	Previous 30 months
Silvereye	Positive	0.382	0.003	Jul–Dec	Previous 1, 2, 3 and 4 years

et al. 1989). Hence, rather than a uniform pattern or congruent declines in ecologically divergent species, insectivores were undergoing disproportionate rates of declines, especially those ground-foraging species considered most sensitive to changes in the availability of prey (Watson 2011).

For those species that increased significantly in abundance, only one (Spotted Pardalote) was among the 20 most abundant species, so these increases reflect small changes in total densities of woodland birds and do not offset the larger losses from declining species. The Spotted Pardalote is one of the most specialised insectivores of the group, feeding almost exclusively on larval psyllids, small sap-sucking insects that increase in abundance on trees experiencing water-stress (Heatwole and Lowman 1986; Watson 2011).

Two of the four species that showed increases were nectarivores, suggesting increases in available resources or shifts in

competitive interactions. This may, however, relate to the location of the survey sites, which were all within 800 m of the homestead garden, with planted native species of *Grevillea*, *Callistemon*, *Correa* and other flowering plants that may have contributed to winter–spring survival or abundance of some birds and the observed increases in the two honeyeater species (see Coates and Harris 2008).

This study reinforces a growing appreciation that declines of woodland birds are not local phenomena, nor are they restricted to fragmented or otherwise disturbed landscapes (Mac Nally *et al.* 2009; Watson 2011). The fact that broad-based declines were found in one of the most intact and extensively forested areas of south-eastern Australia points to the influence of pervasive regional processes. Indeed, declines are not restricted to birds, with reductions in abundance and distributional ranges and local extinctions recorded in several other taxa (e.g. fossorial marsu-

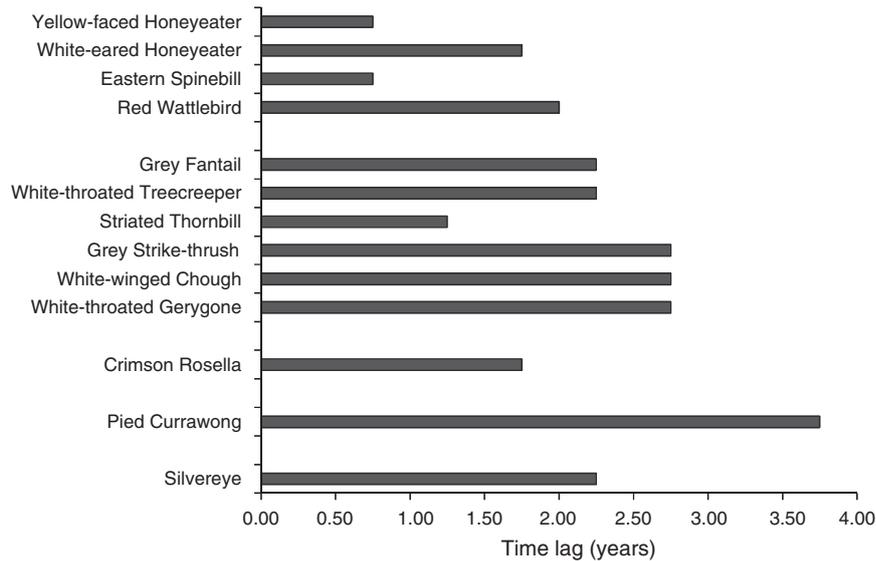


Fig. 4. Time-lag (years) between rainfall and maximum effect on abundances of various bird species.

pials and snakes) in these woodlands and forests (Watson 2011), symptomatic of the effect of regional processes rather than the effect of local species interactions.

Reduced rainfall as a driver of population declines

We suggest that reduced summer–autumn rainfall is the most likely explanation for the recorded declines in woodland birds, with changes in avian occurrence reflecting broad-based changes in availability of food. The period in which we collected our data coincided with one of the most prolonged and severe droughts recorded for Australia (CSIRO 2010). In addition, there was a long-term downward trend in January–June rainfall, shown in this study to be the most important factor determining local abundances of small insectivores. This declining trend in January–June rainfall is consistent with long-term observations across a much wider area (the Murray–Darling Basin, which encompasses the study area), now being attributed to climate change (CSIRO 2010). Future conditions are likely to be drier and warmer than the long-term historical climate averages of south-eastern Australia (CSIRO 2010). For western New South Wales (NSW), including the study area, an increase in evaporation across most of the region is projected to create drier conditions throughout the year (DECC 2008).

Low rainfall and drought have been implicated in driving bird declines in other studies. Mac Nally *et al.* (2009) concluded that a severe lack of rain (a 40% decline in rainfall since the 1950s and a drought since 1996), accompanied by a rise in mean annual temperature, led to reduced availability of all types of food and low breeding success among a wide range of birds in northern Victoria, south-eastern Australia. Thus, habitat quality declined even though the region did not experience a significant loss of woody vegetation in recent decades. In other parts of southern Australia, low food availability coincident with more severe and prolonged droughts appears to be driving bird declines. Reid (1999) noted that small birds often did not recover after severe droughts in the sheep–wheat belt of NSW, and changes in

woodland bird abundance around Cowra, southern NSW, were thought to reflect differing levels of food resources over time, with food limitation likely to be driving declines in many woodland-dependent species (Reid and Cunningham 2008).

Rather than affecting all food sources equally, reduced rainfall (especially during the summer) has the greatest effect on litter-dwelling arthropods (Watson 2011). Indeed, there is evidence that trees experiencing water stress may be more vulnerable to attack by psyllids and other canopy-dwelling arthropods, consistent with recorded patterns of increases in foliage-gleaning species reported here and elsewhere (Reid 1999; Watson 2011 and references therein). In contrast, arthropods living in the litter and soil are highly sensitive to soil moisture and, although they exhibit a variety of strategies to survive seasonal dry periods, the effect of prolonged drought on these communities has not been studied. We suggest that reductions in rainfall and increased variability in rainfall will have the most acute effects on these epigeic arthropods, in turn shifting woodland food webs to favour canopy-foraging insectivores over their ground-feeding counterparts.

Breeding by forest or woodland birds can be reduced in dry years and severely restricted in droughts (Keast 1959; Nias and Ford 1992; Rowley and Russell 1993; Stevens and Watson 2006). Reduced reproductive output can also be linked directly to food supply (Zanette *et al.* 2000). Our system is one with inherently low productivity, and is therefore particularly susceptible to drought stress, with associated effects on birds. Though small Australian passerines tend to be long-lived, they have low reproductive rates, and hence an inability to recover rapidly following a disaster (Yom-Tov 1987; Rowley and Russell 1991; Yom-Tov *et al.* 1992). A prolonged 6-year drought, with associated depressed food availability and breeding activity, is likely to result in many species falling below the abundance needed for local population viability. Although some birds may move to refuges within large regional patches of vegetation such as the Pilliga Forest in drought conditions, there are fewer such refuges owing to historical clearing of better-quality land.

We recognise that several other processes may contribute to the declines reported here. Although Noisy Miners are known to have an adverse effect on avian populations (Maron *et al.* 2011), this species was comparatively rare in the study area (ranked 48 of 84 species in terms of density), and aggressive interactions were rarely recorded. Nonetheless, Noisy Miners increased in abundance and reporting rate since they were first detected in the study area in 2000 and could exclude insectivorous species if they become more abundant in the future. Another possible explanation for the observed declines is 'extinction debt': the time-lag between loss of habitat and local extinctions (Tilman *et al.* 1994; Szabo *et al.* 2011). The nature and tempo of declines expected under this model differ from those reported, with a gradual and accelerating loss of species expected through time. Moreover, this alternative explanation does not account for the disproportionate loss of insectivorous species nor the recorded increases in some species. Extinction debt and other legacies of subtle shifts in land-use or broadscale habitat clearing north of the study area may contribute to the reported long-term declines, but we consider their influence to be more diffuse than the marked effects of rainfall on food availability we detected.

Prospect

Rather than an idiosyncratic finding or a pattern unique to southern Australian woodlands, we suggest that food limitation associated with reduced rainfall is a more generalised phenomenon, interacting with other stressors to limit populations and simplify ecological communities. The heightened sensitivity of insectivorous species is also considered a widespread phenomenon, highlighting how little is known about below-ground invertebrate communities and their linkages with above-ground food-webs (Watson 2011). We suggest that food limitation for ground-foraging insectivores underlies many of the reported declines in farmland birds in Europe (Fuller *et al.* 1995; Donald *et al.* 2001) and elsewhere, interacting with other consequences of land-use intensification to reduce the food resources available to these species. Although these patterns have been most marked in birds, many other groups of insectivores are likely to show similar trends, with local extinctions expected to be more frequent for less vagile groups like small mammals and understorey reptiles (Watson 2010).

The observed declines reinforce the realisation that large areas of intact native vegetation are not necessarily sufficient to maintain viable populations of native birds, given the preferential clearing of the most productive habitats, intensification of land-use in the matrix surrounding remnants, and changing climatic regimes altering availability of critical resources (Bennett and Watson 2011). Rather than a landscape-scale pattern associated with habitat fragmentation and change in land-use, the fact that dramatic declines in woodland-dependent birds are also occurring in more intact, continuously forested regions suggests it is an ecosystem-wide phenomenon. There is now an urgent need to conserve and rehabilitate the most productive habitats as refuges for birds in times of stress, such as drought, and to maximise functional landscape connectivity between these productive areas and the more extensive tracts of woodland in lower productivity landforms. Those few remaining woodlands growing on floodplains and other areas with more consistent soil moisture will

become increasingly important foci for local and catchment-scale conservation, acting as refuges during periods of scarcity. Rather than being managed in isolation, however, our research supports the need to integrate on-ground actions at regional and larger scales, maximising linkages between remaining high-quality areas and to give priority to restoration efforts in strategic gaps.

Postscript

A severe bushfire that began on 12 January 2013 affected the study region, burning more than 43 000 ha of the Warrumbungle National Park, including the three study areas and the senior author's property. Post-fire surveys of birds have already begun.

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