Riparian tree cover enhances the resistance and stability of woodland bird communities during an extreme climatic event

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Summary
1. Ecosystems world-wide increasingly are subject to multiple interacting disturbances. Biodiversity in anthropogenic landscapes can be enhanced by manipulating landscape patterns, but could such landscape management also assist biota to cope with the effects of extreme climatic events, such as drought?
2. We surveyed woodland bird communities in 24 ‘whole’ landscapes (each 100 km²) in an agricultural region of south-eastern Australia near the beginning (2002–2003), middle (2006–2007) and after (2011–2012) an extreme drought (the ‘Millennium Drought’). We quantified the resistance, resilience and stability of the avifauna to the decade of drought and related these measures to properties of the study landscapes: the extent of wooded habitat, configuration of habitat, land-use composition, landscape productivity and geographic context.
3. Landscape productivity, represented by the extent of riparian tree cover in the landscape, was the strongest driver of the resistance, resilience and stability of avifaunal richness to severe drought. Woodland bird communities in landscapes with larger areas of riparian tree cover retained a larger proportion of their species richness during the Millennium Drought and consequently had greater stability over the drought’s duration.

4. Synthesis and applications. Landscape properties can influence the resistance, resilience and stability of faunal communities to an extreme climatic event. By protecting, restoring and enhancing native vegetation in productive areas of landscapes along stream systems, drainage lines and floodplains, land managers can effectively build climatic refugia and thereby enhance the resistance of biota to climatic extremes. However, a net decline over the entire study period suggests this will not, by itself, arrest decline during periods of extreme drought.

Key-words: avifauna, climatic extremes, drought, fragmentation, resilience, resistance, riparian vegetation, stability

Introduction
Globally, ecosystems are increasingly subject to multiple, often interacting disturbances (e.g. vegetation clearing, exotic species and drought) that operate at different spatial and temporal scales (Brook, Sodhi & Bradshaw 2008; Doherty et al. 2015). Prominent among these is the interaction between human modification of landscapes and the consequences of a changing climate (Malhi et al. 2008; McAlpine et al. 2009). Landscape change, through the loss, fragmentation and replacement of natural vegetation, is a primary cause of the global loss of biodiversity (Foley et al. 2005; Ramankutty et al. 2008). Today, the biota of modified landscapes must cope not only with altered patterns of habitat and new land uses, but also with an increasing frequency of extreme climatic events, such as long-term droughts or heatwaves (IPCC 2013).
While much attention has been given to identifying landscape properties that enhance biodiversity in modified environments (Fahrig 2003; Fischer & Lindenmayer 2007; Tscharntke et al. 2012), this knowledge is derived largely from static or ‘snapshot’ studies that relate patterns in biodiversity at a given point in time to the attributes of landscapes. Such studies have provided powerful insights into the role of landscape properties, such as the extent, configuration and composition of landscape elements, in driving patterns of biodiversity (Villard, Trzcinski & Merriam 1999; Mortelliti et al. 2010). Much less certain, but increasingly important, is the role that such landscape properties could play in buffering ecological communities from the impacts of an increasingly variable climate (Mac Nally et al. 2014).

The change that occurs in an ecological community during and following disturbance, such as climatic extremes, can be conceptualized and measured in a variety of ways (Nimmo et al. 2015). Three measures of particular relevance to biodiversity conservation are resistance, resilience and stability. Resistance refers to the magnitude and direction of change that a community or ecosystem experiences during a disturbance (Connell & Sousa 1983; Tilman & Downing 1994). Communities with high resistance are more able to withstand a disturbance (Nimmo et al. 2015). Resilience refers to community change following disturbance, usually focused on the ability of a system to ‘bounce back’ after a disturbance (e.g. Bruelheide & Luginbühl 2009; Mac Nally et al. 2014). Communities with high resilience can recover to a greater extent, or more rapidly, following the release of a disturbance (Lake 2013; Bennett et al. 2014). Stability can be defined as the constancy in a community measure (e.g. species richness) over the duration of a disturbance (Donohue et al. 2013). Communities with high stability display less variability over the course of a disturbance. Thus, resistance, resilience and stability are three measures of change which, if enhanced, would improve the capacity of communities to withstand the impacts of disturbance events, such as climatic extremes (Nimmo et al. 2015).

To quantify the influence of landscape properties on ecological change during climatic extremes, at least two requirements must be met. First, it is necessary to quantify change in the biota throughout the trajectory of the climatic extreme event. Secondly, such change must be measured across multiple independent landscapes (Fahrig 2003), in order to relate variation in change to differences in landscape attributes. This requires that both the measure of ecological change and the properties of landscapes are characterized for entire landscapes (i.e. a ‘whole-of-landscape’ design, sensu Bennett, Radford & Haslem 2006).

Here, we use a long-term data set to examine change in woodland bird communities in south-eastern Australia during a severe drought. The status of woodland birds in Australia is of much concern as numerous species have experienced historical and ongoing decline (Ford 2011). We systematically sampled woodland birds in a series of independent landscapes, each 100 km² in size, chosen to represent a gradient in human modification from landscapes with large amounts of remnant woodland to heavily modified landscapes with <2% native vegetation remaining (Radford, Bennett & Cheers 2005). We sampled the avifauna near the beginning, in the middle and after the abrupt end of a decade of severe, record-breaking drought: the ‘Millennium Drought’ (Van Dijk et al. 2013). We used these data to quantify the resistance, resilience and stability of woodland bird communities over the course of the drought and related these measures to spatial properties of the study landscapes. Our primary aim was to determine whether landscape properties can mediate changes in woodland bird communities associated with an extreme climatic event.

Materials and methods

STUDY AREA

The study area encompasses 20 500 km² of north-central Victoria, Australia. The region experiences a temperate climate with hot summers and mild winters; mean annual rainfall ranges from 400 to 670 mm. Native vegetation is characterized by eucalypt forests and woodlands with a relatively open canopy, 10–25 m in height. The vegetation has been cleared for farming (pastoral, cropping and horticulture) over the last 150 years, and only 1.17% of the region’s original tree cover remains (ECC 1997).

STUDY DESIGN

The sampling protocol initially was established to examine how woodland bird communities respond to the extent, configuration and composition of wooded vegetation at the landscape scale (Radford, Bennett & Cheers 2005). The study design involved 24 landscapes, each 100 km², stratified according to i) the proportional extent of wooded cover (range = 2–60% of the landscape) and ii) the configuration of wooded cover (from highly aggregated to dispersed across the landscape) (Fig. 1). This whole-of-landscape approach means that each 100 km² landscape is an independent data point for analysis. Tree cover was quantified using a digital tree cover map with a grid-cell resolution of 10 × 10 m (Radford, Bennett & Cheers 2005). Ten survey sites were located in wooded vegetation in each landscape: three were in riparian vegetation, and the remaining seven were allocated according to the proportional cover of different types of landscape elements (i.e. roadside strips, small and large remnants, scattered trees). Landscapes were selected to avoid towns and large wetlands and to minimize variation in vegetation composition and topography. Although some restoration planting is occurring on farms, recent change in tree cover at the landscape scale is minimal (e.g. <0.5% from 1990 to 2008; Kyle & Duncan 2012).

LONG-TERM SAMPLING

In 2002–2003, four rounds of bird surveys were conducted at each of the 240 survey sites (24 landscapes X 10 sites). In each survey round, a 30-min survey was undertaken on a 2-ha fixed-width line transect (see Radford, Bennett & Cheers 2005). Survey rounds were undertaken twice in spring (breeding season) and once each in autumn and winter (i.e. in total, 40 surveys per
landscape and 960 surveys overall). This equates to a total of 20 h survey effort within each of the 24 study landscapes. In both 2006–2007 and 2011–2012, all 24 landscapes were resurveyed for another 20 h using the same field methods as in 2002–2003, undertaken by the same experienced ornithologist, who carried out half of the 2002–2003 surveys. Allocation of surveys across seasons was similar to the original sampling design (i.e. two surveys in spring/early summer, and one each in autumn and winter).

The three sampling periods (2002–2003, 2006–2007 and 2011–2012) occurred during and following the ‘Millennium Drought’ in south-eastern Australia, which ran from 2001 to 2009 (Van Dijk et al. 2013), and has been described as the worst drought in Australia’s instrumental record, including the longest period of consecutive below-median rainfall years across south-eastern Australia since 1900 (Van Dijk et al. 2013). Such droughts correspond with El Niño episodes, which are predicted to increase in intensity with future climate change (Power et al. 2013). The initial sampling period (2002–2003) corresponded with the onset of the drought (i.e. c. 1 year after the drought began). The second period (2006–2007) occurred 5–6 years into the drought and 2–3 years before the drought ended. The effect of the drought on the avifauna at this time was severe: two-thirds of terrestrial species experienced substantial regional decline (Mac Nally et al. 2009). The third sampling period (2011–2012) occurred after the drought broke following flooding rains in 2010 and 2011 (Fig. 1). While the reporting rates of some species (29%) increased in response to the rains, more than half of all terrestrial species (55%) had not recovered from the drought (Bennett et al. 2014). We refer to these three periods as ‘early drought’, ‘mid-drought’ and ‘post-drought’, respectively.

Because our first sampling period occurred shortly after the drought began, and because our mid-drought measures were taken c. 2–3 years prior to the drought ending, they are likely to be underestimates of the full effect of drought on these communities. By the same token, because the sampled communities may have continued to decline following our mid-drought sampling (i.e. as the drought continued for two more years), our measures of recovery are likely to be underestimates of the degree to which these communities have recovered from the deepest points of their declines.

MEASURING RESISTANCE, RESILIENCE AND STABILITY

We defined resistance as the magnitude and direction of change in community measures (e.g. species richness) experienced during disturbance; resilience, as the magnitude and direction of change following the release of the disturbance; and stability, as the constancy in the community measure over the duration of disturbance. We quantified these measures for two community attributes – species richness and mean species’ incidence (reporting rate) – of woodland-dependent birds, those species that depend on wooded vegetation (Radford, Bennett & Cheers 2005). Our emphasis was on simple indices that are readily interpretable measures of community change and relevant to conservation managers.

To calculate landscape-scale change in species richness, we summed the number of species recorded in a landscape over the course of the 40 surveys in each time period. We included only those species recorded in two or more of the 40 surveys per landscape in any given survey period (i.e. ‘singletons’ were excluded).
Next, we generated values for resistance and resilience based on the proportional change in species richness between periods. Resistance relates to the proportional change between early and mid-drought, and resilience relates to the proportional change from mid-drought to post-drought. We focus on proportional change, rather than absolute change, because it controls, in part, for the differing initial states of the communities that are themselves influenced by landscape properties (Radford, Bennett & Cheers 2005; Nimmo et al. 2015). Thus,

\[
\text{Resistance} = \frac{\text{SR}_{T_2}}{\text{SR}_{T_1}}
\]

and

\[
\text{Resilience} = \frac{\text{SR}_{T_3}}{\text{SR}_{T_1}}
\]

where SR refers to species richness, \(T_1\) to early-drought, \(T_2\) to mid-drought and \(T_3\) to post-drought sampling periods.

Stability was quantified by the coefficient of variation of each measure (species richness or mean incidence) over the three time periods for each landscape, adjusted for small sample size. We subtracted the maximum value from all values to reverse the ordering, such that the landscape with lowest stability (greatest variation in community measures over time) had a value of zero and landscapes with greater stability (less variation in communities over time) had higher values.

Finally, to assess the extent to which the avifaunal community post-drought had recovered relative to that in early drought, a measure of ‘net change’ was calculated for each landscape to represent the proportional change between the first \((T_1)\) and final \((T_3)\) time periods;

\[
\text{Net change} = \frac{\text{SR}_{T_3} - \text{SR}_{T_1}}{\text{SR}_{T_1}}.
\]

We used the same approach to the steps above to measure proportional change between periods for the second community attribute, the mean landscape-scale incidence of all woodland species. Incidence, or reporting rate, refers to the number of surveys (out of 40) in which a species was recorded in a landscape for a given sampling period. Mean incidence is the average of this value across all species for a given landscape.

### Hypotheses and Predictor Variables

We proposed five hypotheses concerning the potential drivers of resistance, resilience and stability in these landscapes (Table 1), largely derived from the findings of static or ‘snapshot’ studies of biodiversity in agricultural land mosaics (Fahrig 2003; Bennett, Radford & Haslem 2006). These hypotheses relate to (i) the total extent of suitable habitat (here, wooded vegetation) in the landscape; (ii) the configuration of habitat; (iii) the composition of land uses in the landscape; (iv) the productivity of the landscape; and v) the geographic context of the landscape (Table 1).

We quantified 10 variables for each landscape to represent these five hypotheses (Table 1). Habitat extent was calculated as the total area of wooded tree cover in a landscape (ha: TREE). The configuration of habitat was quantified by three

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Predictor variable</th>
<th>Name</th>
<th>Description (unit)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat extent</td>
<td>Tree cover</td>
<td>TREE</td>
<td>Total area of tree cover per landscape (ha); a measure of the extent of habitat</td>
</tr>
<tr>
<td>Configuration</td>
<td>Number of patches†</td>
<td>NP</td>
<td>Number of patches of wooded vegetation</td>
</tr>
<tr>
<td></td>
<td>Large patch index</td>
<td>LPI</td>
<td>Percentage of total tree cover contained within the largest single patch in the landscape</td>
</tr>
<tr>
<td></td>
<td>Area-weighted mean of related circumscribing circle</td>
<td>CIRCLE</td>
<td>The area-weighted mean of CIRCLE for all patches in the landscape, where CIRCLE = 1 - (patch area/area of smallest circumscribing circle). CIRCLE increases as patches become more irregular and elongated</td>
</tr>
<tr>
<td>Composition</td>
<td>Land-use component 1</td>
<td>LUSE</td>
<td>First factor derived from a principal components analysis based on proportional cover of production-dominated land-use types; representing a gradient from cropping landscapes (dryland cropping loading = -0.65) to grazing landscapes (grazing land loading = 0.74).</td>
</tr>
<tr>
<td>Vegetation diversity</td>
<td></td>
<td>EVCDIV</td>
<td>Shannon–Wiener diversity index (H’) of the proportional cover of Ecological Vegetation Classes within the wooded portion of the landscape (i.e. within TREE)</td>
</tr>
<tr>
<td>Productivity</td>
<td>Riparian tree cover</td>
<td>RIPAR</td>
<td>Total area of wooded vegetation classes typical of streamside and adjacent floodplains, per landscape (ha); a measure of the amount of vegetation of naturally higher fertility/moisture</td>
</tr>
<tr>
<td></td>
<td>Normalized difference vegetation index</td>
<td>NDVI</td>
<td>Derived from the reflectance of the electromagnetic spectrum near the infrared and red portions, values averaged across the 10 sites per landscape over 12 years (2000–2012); a measure of vegetation ‘greeness’, ranging from 0 (low productivity) to 1 (high productivity)</td>
</tr>
<tr>
<td>Context</td>
<td>Geographic location</td>
<td>EAST</td>
<td>Easting coordinate of the centre of each landscape (m)</td>
</tr>
<tr>
<td></td>
<td>Distance to large forest</td>
<td>SOURCE</td>
<td>Mean distance (km) across sites to the closest large (&gt;10 000 ha) forest block</td>
</tr>
</tbody>
</table>

†Derived from Fragstats (McGarigal & Cushman 2002).
variables: a measure of subdivision of habitat (number of vegetation patches: NP), the aggregation of habitat (large patch index: LPI) and the shape complexity of habitat patches (CIRCLE) (see Table 1 for further description). Landscape composition was measured by using two variables: an index of the dominant agricultural land use (derived from a principal components analysis: LUSE) and the diversity of native vegetation types within the landscape (EVCDIV) (Table 1). We used two variables to represent the productivity of landscapes. The total area of riparian tree cover (ha: RIPAR) represents the amount of wooded habitat occurring on more mesic sites with more fertile soils. The normalized difference vegetation index is a measure of vegetation ‘greenness’ (mean value for the 10 survey sites: NDVI). A final two variables quantified the geographic context of the landscape: geographic location (eastern coordinate of the landscape centre: EAST) and the distance to the closest large (>10 000 ha) block of native vegetation that serves as a potential source for bird populations (mean distance for the 10 sites, km: SOURCE). Variables were standardized (mean = 0, SD = 1) to allow a direct comparison of variable coefficients.

STATISTICAL ANALYSIS

All analyses were implemented in R version 2.11.1 (R Development Core Team 2013).

We measured pairwise collinearity among predictor variables with Spearman’s rank correlations. Levels of pairwise collinearity were moderate to low, with all coefficients <0.7, a general threshold above which parameter estimates become particularly unreliable (Dormann et al. 2013). All measures of avifaunal change were modelled assuming a Gaussian distribution of errors and an identity link function. Predictor variables were log-transformed prior to model selection to improve fit where appropriate.

We employed an information theoretic approach to evaluate the level of support for each of the five hypotheses with Spearman’s rank correlations. Levels of pairwise collinearity were moderate to low, with all coefficients <0.7, a general threshold above which parameter estimates become particularly unreliable (Dormann et al. 2013). All measures of avifaunal change were modelled assuming a Gaussian distribution of errors and an identity link function. Predictor variables were log-transformed prior to model selection to improve fit where appropriate.

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As there was no clearly best model (wi < 0.9) (Appendix S3), model averaging was undertaken for all response variables.

Resistance

Only one model received substantial support (Δwi < 2) for explaining variation in the resistance of species richness across study landscapes. This model included only the productivity hypothesis (Appendix S3) and explained half of the variance in the data (i.e. \( R^2 = 0.50 \)). For resistance of mean incidence, the best model included the productivity and configuration hypotheses (Appendix S3). This model explained a large proportion of variance in the data (\( R^2 = 0.78 \)). Summed weights showed the productivity hypothesis received by far the greatest support with \( \sum wi = 0.99 \) for models describing resistance for both species richness and mean incidence (Fig. 2). For mean incidence, configuration was also well supported \( \sum wi = 0.98 \);
All other hypotheses received little support (generally $\sum w_i < 0.2$).

Model averaging revealed that the total extent of riparian tree cover in a landscape – a measure of productivity (Table 1) – had a strong, positive effect on resistance in relation to species richness, as indicated by a 95% CI that did not overlap zero (Fig. 3). Landscapes with a greater amount of riparian tree cover retained a greater proportion of their initial species richness during drought (Fig. 4). All other predictors had a less certain influence, with 95% CIs overlapping zero (Fig. 3). The extent of riparian tree cover also had a strong and positive effect on resistance to drought for mean species incidence: landscapes with greater extent of riparian tree cover retained a higher proportion of the initial mean incidence of woodland birds, reflecting a smaller proportional decline in the abundance of species. One variable representing configuration also influenced the resistance of mean species incidence (Fig. 3); the aggregation of habitat (LPI) had a strong negative influence on the resistance of mean incidence (Fig. 3). Landscapes in which tree cover was more aggregated had less resistance to decline in the mean incidence of woodland species.

**Resilience**

The productivity hypothesis was the top ranked model explaining resilience of species richness and mean incidence (Appendix S3), explaining 37% and 43% of the variance in the data, respectively. The productivity hypothesis again received the greatest support for explaining resilience for both species richness ($\sum w_i = 0.75$) and mean incidence ($\sum w_i = 0.98$) (Fig. 3). There was little support for any other hypotheses for either species richness or mean incidence (Fig. 3). Model averaging showed that the direction of effects tended to be the opposite of those found for resistance (Fig. 3). For both response variables, the only predictor with 95% CIs not overlapping zero was the extent of riparian tree cover in the landscape (Fig. 3). Landscapes with a greater extent of riparian tree cover displayed a lower level of resilience in relation to species richness and mean incidence of woodland birds (Fig. 4).

**Stability**

The productivity hypothesis was the top ranked model in explaining the stability of species richness through the duration of the drought, explaining 50% of the variance in stability (Appendix S3). For mean incidence, the best model explained 70% of the variance and included the productivity and configuration hypotheses (Appendix S3). The productivity hypothesis received strong support for explaining community stability, as indicated by $\sum w_i$ of 0.99 and 0.97 for species richness and mean incidence, respectively (Fig. 2). The configuration hypothesis was also supported for stability in mean incidence, with $\sum w_i = 0.99$. No other hypothesis received substantial support ($\sum w_i < 0.40$). Model averaging showed that the extent of riparian vegetation had a positive influence on stability for both species richness and mean incidence, while aggregation of habitat (LPI) had a negative influence on stability for the mean incidence of woodland bird species (Fig. 3).

**Net change**

The null model (i.e. intercept only) was the highest ranked model for explaining net change in species richness (Appendix S3), whereas the configuration hypothesis received most support for mean incidence ($R^2 = 0.15$).

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None of the hypotheses received support in relation to net change in species richness, with the highest $\sum w_i$ for any hypothesis being 0.32 (for configuration) (Fig. 2). For net change in mean incidence of woodland species, there was strong support for the configuration hypothesis ($\sum w_i = 0.99$; Fig. 2), but little support for others. Model averaging confirmed the limited influence of predictor variables on net change in both species richness and mean incidence, with only LPI having a 95% CI that did not overlap zero. Proportional change in species richness and mean incidence over the duration of drought (early drought to post-drought) was greater in landscapes with more aggregated wooded habitat (Fig. 3), such that those landscapes with more aggregated tree cover had the (proportionally) greatest declines.

**Discussion**

Understanding the factors that influence the response of ecological communities to climatic extremes is pivotal to biodiversity conservation in a changing climate (Morecroft et al. 2012). It is particularly important in anthropogenically modified landscapes, where climatic extremes (droughts, heatwaves, floods) are imposed on a biota already undergoing transformation as a consequence of landscape change (Mac Nally et al. 2009; Haslem et al. 2015; Nimmo et al. 2015). A key finding from this work was that the resistance, resilience and stability of avifaunal communities to severe drought were associated with the spatial properties of landscapes in a highly modified agricultural region. These results highlight the potential for management actions undertaken at landscape or regional scales to ameliorate the impacts of more global stressors, such as the increasingly severe climatic extremes predicted to accompany climate change.

Previous work in the study area documented a ‘collapse’ of the region’s avifauna during the Millennium Drought, with two-thirds of species reported to have substantially declined across the 24 study landscapes examined here (Mac Nally et al. 2009). Follow-up work showed that this decline was only partly reversed in the 2 years following the end of the Millennium Drought and that for many species, declines were ongoing (Bennett et al. 2014). These studies observed declines in all landscapes, including those with large blocks of native vegetation in conservation reserves, but did not go further...
to identify spatial patterns associated with decline or recovery. Such spatial patterns would emerge if particular components of the landscape either ameliorated or enhanced the decline, for example by buffering communities against the influence of drought (e.g. providing ‘drought refuges’; Mackey et al. 2012). A key finding in this study is that there are spatial patterns in the resistance and resilience of biodiversity to changes associated with extreme, long-term drought, and these patterns relate to landscape properties that can be manipulated by land management.

Landscape productivity, as measured by the extent of riparian tree cover in a landscape, was a particularly important influence on the proportional change in avifaunal assemblages associated with severe drought. Riparian tree cover ranges from broad stands (e.g. >100 m wide) adjacent to perennial rivers to narrow strips of trees (10–25 m wide) along seasonally dry streams (first- and second-order streams) through farmland. The overall extent of such vegetation in the landscape was strongly associated with heightened resistance, such that the avifaunal richness and mean incidence of species were more stable. Together, increased resistance and stability point to the critical role that vegetation on moister, fertile soils can play in acting as a refuge in dry environments during severe long-term drought (Mackey et al. 2012).

At least three mechanisms could be responsible for the effect of riparian tree cover on resistance. First, although drought will also negatively affect vegetation on productive soils, the availability of key resources for bird species (e.g. food, structural complexity) is likely to be more stable and remain relatively high compared with woodlands on drier, less fertile soils (Ballinger & Lake 2006). Secondly, due to their relatively higher productivity, riparian sites may harbour larger bird populations prior to the drought, buffering populations from the loss of individuals or a failure to recruit as the drought took hold. Finally, by occurring as a connected network along stream systems, riparian vegetation enhances connectivity through cleared farmland for bird species dependent on wooded vegetation. Notably, three of the six study landscapes with highest overall extent of riparian tree cover encompassed the Goulburn River and its floodplain (mostly cleared), a perennial river that provides a major, north–south vegetated corridor through the region.

By conferring greater landscape-level stability, more productive landscapes ensure the ongoing provision of ecosystem services and ecological functions performed by birds (Sekercioglu 2006). In a static sense, riparian tree cover provides a relatively rich habitat for woodland birds and supports distinctive communities (Palmer & Bennett 2006), and, at the landscape scale, riparian vegetation adds unique species to the landscape pool, particularly in heavily modified environments (Bennett, Nimmo & Radford 2014). Retention, restoration and expansion of native vegetation along streams and adjacent floodplains have multiple benefits (Gregory et al. 1991; Naiman, Decamps & Pollock 1993) and must be a priority for conservation in heavily modified regions.

Landscape configuration also was a well-supported hypothesis explaining several measures of avifaunal change. Net change in both species richness and mean incidence over the duration of sampling was proportionally greater (i.e. more decline) in landscapes with more aggregated vegetation. Further, for mean incidence of woodland birds, landscapes with aggregated tree cover fewer tended to have lower resistance, but similar resilience as landscapes with more dispersed tree cover. That is, in aggregated landscapes there was a greater proportional decline in mean incidence during drought, and this failed to recover post-drought. As incidence is a surrogate for abundance, this suggests greater proportional declines in species’ populations in more aggregated landscapes.

The negative impact of habitat aggregation on the resistance of mean incidence was unexpected, as Bennett et al. (2013) recently showed greater drought-induced habitat degradation in fragments compared with more continuous woodlands in the study region. One explanation is that larger, more aggregated tracts of remnant vegetation in this and other agricultural regions typically occur on drier, less productive soils (Maron et al. 2012). Thus, the capacity of landscapes with more dispersed vegetation to
retain higher abundances may be a further, albeit indirect, effect of primary productivity. A second possibility is that reduced resistance may reflect management of large continuous remnants, which generally occur on public land. Many of these large reserves have experienced timber and firewood harvesting over the last century. A final potential explanation is that drought might exacerbate population decline occurring over longer time-scales, such as ongoing species relaxation following land clearing in the past (Vellend et al. 2006). Under scenarios of extinction debt, larger patches of habitat are expected to lose populations more slowly than smaller patches (Gonzalez 2000). Thus, drought could exacerbate, or ‘speed up’, the realization of extinction debt.

A caveat of this study is that our models are correlative and lack true spatial controls. This will often be the case for large-scale empirical work on climatic extremes because of the inherent infeasibility of manipulating long-term climate at regional scales. Our findings could be further validated by conducting smaller-scale manipulative studies that mimic drought and examine responses of taxa of smaller size and lower mobility across productivity and disturbance gradients (see Thrush et al. 2009), or by corroborating our findings using mechanistic models (Kearney & Porter 2009).

**IMPLICATIONS AND CONCLUSIONS**

This study, together with the previous work in this region (Radford, Bennett & Cheers 2005; Bennett, Nimmo & Radford 2014), endorses a clear message for the restoration of agricultural landscapes in the face of an increasingly variable climate. First, a key consideration is the overall extent of wooded vegetation (i.e. suitable habitat) in the landscape, which is the primary determinant of the landscape-scale richness of woodland bird species (Radford, Bennett & Cheers 2005). Secondly, to enhance the ability of bird communities to absorb the effects of severe drought, a priority is to ensure that tree cover in the more fertile and productive parts of the landscape, such as along streams and drainage lines, is retained, restored and extended. These two principles together suggest that increasing the extent of tree cover on riparian sites will increase both the number of species in a landscape and the proportion of those species that are retained during drought. Such actions will have many other benefits, for example for aquatic ecosystems, water quality and landscape aesthetics (Gregory et al. 1991; Naiman, Decamps & Pollock 1993).

It is important to recognize that the avifauna of these landscapes tended not to recover fully following the breaking of the drought, at least within the first 2 years (Bennett et al. 2014). It is likely that recovery is ongoing, particularly given the relatively low reproductive rates of many Australian passerines (Yom-Tov 1987). Continued monitoring will be essential to describe any further recovery. However, such losses over the course of a single drought cycle, if sustained, will lead incrementally to much greater declines over successive drought cycles. Such long-term loss is unlikely to be reversed without a sustained commitment to restoration actions.

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**Data accessibility**

Raw data are provided in Appendices S1 and S2.

**References**


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Supporting Information

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

Appendix S1. Number of landscapes in which woodland bird species were recorded in each of three survey periods: T1 (2002/2003; early drought), T2 (2006/2007; mid drought) and T3 (2011/2012; post drought).

Appendix S2. Species richness and mean incidence for study landscapes in each of the three time periods.

Appendix S3. Model selection for the drivers of resistance, resilience, stability and net change of woodland bird species richness and mean incidence during the Millennium Drought, ranked according to Akaike’s Information Criterion adjusted for small samples sizes (AICc).