

Landscape properties mediate the homogenization of bird assemblages during climatic extremes

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Abstract. Extreme weather events, such as drought, have marked impacts on biotic communities. In many regions, a predicted increase in occurrence of such events will be imposed on landscapes already heavily modified by human land use. There is an urgency, therefore, to understand the way in which the effects of such events may be exacerbated, or moderated, by different patterns of landscape change. We used empirical data on woodland-dependent birds in southeast Australia, collected during and after a severe drought, to document temporal change in the composition of bird assemblages in 24 landscapes (each 100 km²) representing a gradient in the cover of native wooded vegetation (from 60% to <2%). We examined (a) whether drought caused region-wide homogenization of the composition of landscape bird assemblages, and (b) whether landscape properties influenced the way assemblages changed in response to drought. To quantify change, we used pairwise indices of assemblage dissimilarity, partitioned into components that represented change in the richness of assemblages and change in the identity of constituent species (turnover). There was widespread loss of woodland birds in response to drought, with only partial recovery following drought-breaking rains. Region-wide, the composition of landscape assemblages became more different over time, primarily caused by turnover-related differentiation. The response of bird assemblages to drought varied between landscapes and was strongly associated with landscape properties. The extent of wooded vegetation had the greatest influence on assemblage change: landscapes with more native vegetation had more stable bird assemblages over time. However, for the component processes of richness- and turnover-related compositional change, measures of landscape productivity had a stronger effect. For example, landscapes with more riparian vegetation maintained more stable assemblages in terms of richness. These results emphasize the importance of the total extent of native vegetation, both overall cover *and* that occurring in productive parts of the landscape, for maintaining bird communities whose composition is resistant to severe drought. While extreme climatic events cannot be prevented, their effects can be ameliorated by managing the pattern of native vegetation in anthropogenic landscapes, with associated benefits for maintaining ecological processes and human well-being.

Key words: agricultural landscape; Australia; community assemblage; drought; extreme climatic event; landscape structure; temporal dynamics; woodland birds.

INTRODUCTION

Faunal assemblages in landscapes heavily modified by human land use are subject to a range of disturbances that influence their structure and composition. Many such disturbances arise rapidly and then are maintained at a relatively constant level: for example, the invasion

of new species (McKinney and Lockwood 1999, Rahel 2000), and the loss and fragmentation of native vegetation (Wiens 1995, Lindenmayer and Fischer 2006). Other disturbances, such as extreme climatic events, are temporally dynamic (McLaughlin et al. 2002), and their effects can be disproportionate to their often short duration (Jentsch et al. 2007, Thibault and Brown 2008). The frequency and magnitude of such climatic events are predicted to increase under climate change scenarios (Easterling et al. 2000), and increasingly their impacts will be experienced in environments subject to sustained anthropogenic change (McLaughlin et al. 2002, Opdam and Wascher 2004). However, despite clear ramifications for biotic function in fragmented systems, the interacting effects of climatic perturbations on community dynamics are not well understood (Thibault and Brown 2008) and difficult to anticipate (Jiguet et al. 2011).

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Disturbance processes can alter the structure and composition of biotic assemblages in a number of ways (Olden 2006, Thibault and Brown 2008). A common finding is that disturbances such as species invasions (Rahel 2000) and urbanization (McKinney 2006) result in an increased similarity of disparate assemblages over time. This is commonly due to increased losses of sensitive species, and a parallel establishment of a smaller number of generalist species. This process has been termed biotic homogenization, with biotic differentiation being the opposite process, where assemblages become more distinct over time (McKinney and Lockwood 1999). Change in assemblages in response to extreme climatic events is harder to predict, due to species-specific variation in the direct and indirect effects of such disturbances (Jiguet et al. 2011), and in rates of post-disturbance recovery (Piessens et al. 2009). Nonetheless, it has been proposed that extreme climatic events such as drought may lead to the homogenization of species assemblages, via a filtering of species intolerant of harsh environmental conditions (Chase 2007).

In modified environments, the response of biota to disturbance events may be exacerbated or moderated by the characteristics of the landscapes they inhabit. Landscape properties influence the occurrence of fauna via a number of different mechanisms. The amount of habitat in the landscape positively influences population size (Bennett et al. 2006), with potential flow-on effects for the capacity of species to withstand disturbances such as drought (see Oliver et al. 2013). Spatial configuration of habitat affects species movements and dispersal (Bennett et al. 2006); for example, Oliver et al. (2013) identified a positive relationship between habitat connectivity and post-drought recovery of butterfly populations. Extreme climatic events alter resources for fauna (Bennett et al. 2013), and so measures of landscape composition may be important as they reflect habitat diversity and the availability of different resources (Tews et al. 2004, Piha et al. 2007). Although the basis for landscape properties altering the response of fauna to climatic events is still largely theoretical (Newson et al. 2014), empirical support is growing (Piha et al. 2007, Oliver et al. 2013, Newson et al. 2014).

Here, we use data on bird occurrence collected from 24 landscape replicates (each 100 km²) in southeast Australia, surveyed three times over a decade. The three survey periods corresponded with the beginning, middle, and end of the most severe drought on record for southeastern Australia: the “Millennium Drought” (van Dijk et al. 2013). Almost two-thirds of individual bird species declined in the region during the drought (Mac Nally et al. 2009). Following drought-breaking rains, recovery occurred for some species, but others have declined further (Bennett et al. 2014b). Here, we examine change in the composition of bird assemblages over this severe climatic perturbation, and use the unique opportunity afforded by the study design to relate such

compositional change to the properties of study landscapes.

We ask the following questions:

- 1) Does the similarity of bird assemblages across landscapes increase or decrease as a result of severe drought, such as would indicate a region-wide homogenization or differentiation, respectively?
- 2) Do landscape properties influence temporal changes in landscape-level bird assemblages in response to an extreme climatic event?

METHODS

Study area

The study area encompasses ~20 500 km² of north-central Victoria, Australia: extending from the riverine plains of the Murray River in the north, to the inland slopes of the Great Dividing Range in the south and east (see Appendix A for map). Climatic conditions are characterized by hot, dry summers, with most rainfall typically in winter and spring (mean annual range, 400–670 mm, although interannual variation can be high; Appendix B). Rainfall and topographic relief increase from west to east across the region.

Native vegetation on the riverine plains comprises grassy and herb-rich eucalypt woodlands dominated by grey box *Eucalyptus microcarpa*, white box *E. albens*, and yellow box *E. melliodora*; while common tree species of the dry eucalypt forests of the inland slopes are grey box, red ironbark *E. tricarpa*, and yellow gum *E. leucoxylon* (ECC 1997). Riparian (streamside) vegetation is dominated by river red gum *E. camaldulensis*. Substantial clearing (~83%) of native vegetation has occurred in the region since European settlement (~1840s) for the purposes of agriculture (cereal cropping, pastoralism), forestry and mining (ECC 1997).

Study design

We employed a whole-of-landscape approach, whereby the sampling unit was an individual landscape, 10 × 10 km in size. Twenty-four landscapes were sampled, selected to represent gradients in the cover (from ~60% to <2%) and aggregation of native wooded vegetation (Radford et al. 2005; also see Appendix A). Landscapes were selected to avoid towns and large wetlands. Ten survey sites were established in each landscape ($n = 240$ total), stratified among five landscape elements: large remnants (>40 ha), small remnants (<40 ha), roadside vegetation, riparian vegetation, and scattered trees in farmland. Three sites were located in riparian vegetation, and the remainder distributed among other elements in proportion to their cover in the landscape (Radford et al. 2005).

Bird surveys

Birds were surveyed at each site by undertaking a 30-min search of a 2-ha fixed-width line-transect (400 × 50

m, or 500×40 m in some linear sites) (Radford et al. 2005). All species seen or heard were recorded as either on- or off-transect. Each site was surveyed four times in a survey period: twice in spring (September–November), and once in autumn (March–April) and in winter (June–July). These data were pooled for the 10 sites in each landscape, including both on- and off-transect records, to represent the species assemblage for that landscape for a particular survey period.

The survey program, comprising 960 bird surveys per survey period (24 landscapes \times 10 sites \times 4 survey rounds), was repeated for three survey periods spanning a decade. Surveys were undertaken in 2002–2003 (T1), 2006–2007 (T2), and 2011–2012 (T3). T1 surveys were undertaken by two observers, one of whom also undertook all surveys in T2 and T3. Over this time, the study region was affected by severe drought from ~2001 to 2009 (24%, on average, below long-term mean annual rainfall), followed by flooding rains in 2010–2011 (44%, on average, above long-term mean annual rainfall) (Appendix B; see also van Dijk et al. 2013). Thus, the survey periods corresponded with conditions of early drought (T1, 2002–2003), mid drought (T2, 2006–2007), and post drought (T3, 2011–2012).

Landscape properties

We used 10 variables to quantify different properties of the study landscapes (Appendix C). Habitat extent was represented by the total area of native wooded vegetation in each landscape (ha: TREE). The spatial configuration of wooded vegetation in landscapes was quantified by using measures of habitat subdivision (number of vegetation patches: SUBDIV), habitat aggregation (large patch index: AGGREG), and the shape-complexity of habitat patches (SHAPE). Landscape composition was measured by indices of the dominant agricultural land use (derived from a Principal Components Analysis: LUSE), and the diversity of native vegetation types within wooded vegetation in each landscape (including wetland-associated communities: VEGDIV). Measures of the natural productivity of landscapes were quantified by the total area of riparian vegetation (ha: RIPAR) and the Normalized Difference Vegetation Index, a measure of vegetation ‘greenness’ (NDVI). Riparian vegetation includes the mapped area of wooded vegetation classes typical of streambanks, floodplains, and wetland margins. The geographic context of each landscape was represented by its location (easting co-ordinate: EAST) and the distance to the nearest large block ($>10\,000$ ha) of native vegetation (SOURCE).

Statistical analyses

We used pairwise dissimilarity indices to quantify differences in woodland bird assemblages between landscapes, and between survey periods. Traditional measures of pairwise dissimilarity (e.g., Jaccard, Sørensen indices) provide a measure of the difference

between species assemblages recorded at sample locations and so represent “broad-sense” beta diversity. Such broad-sense measures comprise two distinct processes that lead to variation in communities among locations: differences in the *richness* of communities and replacement or turnover in the *identity* of the constituent species (Baiser et al. 2012, Legendre 2014). Richness-related variation relates to differences between locations in the number of species in assemblages, irrespective of their identity. Turnover-related variation quantifies the degree to which species in one location are substituted for by different species in another location. Broad-sense measures of beta diversity can be additively partitioned into these component processes as follows (Carvalho et al. 2012):

$$\beta \text{ (broad-sense)} = \beta \text{ (richness)} + \beta \text{ (turnover)}.$$

Carvalho et al. (2012) presented a method of calculating all three dissimilarity measures using the Jaccard index. We used their approach to quantify the dissimilarity of bird assemblages between (1) landscapes (for the three survey periods separately), and (2) survey periods (for all 24 landscapes separately). We calculated the three dissimilarity measures using presence/absence data for woodland-dependent species recorded in 2 or more of the 40 surveys per landscape in any given survey period (i.e., singletons were excluded). We focus specifically on woodland birds (those primarily associated with woodland/forest vegetation for daily activities), as they are of particular conservation concern (Bennett and Watson 2011). Dissimilarity matrices were calculated using the vegan package v.2.0-7 in R v.2.15.3 (R Development Core Team 2013).

To assess whether the similarity of bird assemblages across landscapes increased or decreased over time, we employed matrix subtraction (see Baiser et al. 2012) using the dissimilarity matrices for each survey period. This process involved subtracting the dissimilarity matrix for the most recent survey period from the matrix for the earlier survey period. This was done for all dissimilarity measures (broad-sense, richness, turnover) for the following change-periods: early to mid-drought (T1–T2), mid to post-drought (T2–T3), and early to post-drought (T1–T3). Positive values in the resultant change matrices indicate an *increase* in pairwise similarity of bird assemblages over time (i.e., homogenization of the woodland bird assemblage); negative values indicate a *decrease* in pairwise similarity (differentiation).

We used a nonmetric multidimensional scaling (NMDS) ordination, based on the broad-sense dissimilarity matrix for all landscapes and survey periods, to illustrate patterns of temporal change in landscape bird assemblages. Rayleigh tests were used to determine if there was a consistent direction of movement of landscape assemblages in ordination space for the T1–T2 and T2–T3 change-periods (i.e., the mean direction of movement differed from random). Mantel tests based

on change matrices were used to compare the correlation between broad-sense similarity and each component measure (richness, turnover) for each change-period. These Mantel results indicated whether change in broad-sense similarity for a given change-period was influenced more strongly by richness-related or turnover-related change.

Generalized linear models were used to examine the relationship between landscape properties and temporal change in landscape bird assemblages. The response variables in these analyses were the three measures of assemblage dissimilarity (broad-sense, richness, turnover) calculated for each landscape (i.e., between survey periods). The same change-periods were examined: T1–T2, T2–T3, and T1–T3. Predictor variables were the 10 variables representing different landscape properties. These variables were grouped according to the type of landscape property they described (habitat extent, configuration, composition, productivity, context; see Appendix C), and thus represent different hypotheses about potential landscape-level influences on change in bird assemblages in response to drought.

We used Akaike's Information Criterion (corrected for small sample sizes, AIC_c [Burnham and Anderson 2002]) to compare the level of support for models representing all possible combinations of these five hypotheses ($n = 31$ models), as well as the hypothesis that landscape properties do not affect temporal change in bird assemblages (i.e., the null model). Akaike weights (w_i) indicate the relative likelihood of a particular model being the most parsimonious of those considered; a $w_i > 0.9$ is required for a model to be selected as the single best at describing the relationship between response and predictor variables. Further, all models within two or four AIC_c values of the best model (that with the lowest AIC_c value) are considered to have substantial support. We summed Akaike weights across all models to provide a measure of the "evidence of importance" for each hypothesis. In cases where all models for a given response variable had $w_i < 0.9$, a single model was produced that included all variables and hypotheses represented in the set of models with substantial support (i.e., $< \Delta_i 4$ of the best model).

Predictor variables were transformed where appropriate (see Appendix C), standardized prior to analysis, and assessed for collinearity (all $r < 0.7$, the level at which collinearity can seriously affect model results [Dormann et al. 2013]). Models were fitted with a Gaussian error distribution and residuals from the global model (i.e., including all variables and hypotheses) were examined to assess model assumptions. Cook's distances (D_i) were used to identify potentially outlying landscapes; landscapes with $D_i > 1$ in the global model were removed from analysis for the associated response variable (see Appendix E). All models were fitted using R v.2.15.3 (R Development Core Team 2013).

RESULTS

Bird occurrence in landscapes

A total of 71 species of woodland birds was recorded across all surveys (excluding singletons; see Appendix D). Species richness per landscape was highest in T1 (mean 29.9 species; range 7–44 species per landscape), lowest in T2 (21.2 species; 9–37 species per landscape), and had increased again by T3 (25.8 species; 8–38 species per landscape). Species showing greatest loss from landscapes between T1 and T2 were often mobile, canopy-feeding nectarivores (e.g., Purple-crowned Lorikeet *Glossopsitta porphyrocephala*, Little Lorikeet *G. pusilla*), whereas ground-foragers (e.g., Painted Button-Quail *Turnix varia*, Red-capped Robin *Petroica goode-novii*) more commonly showed increased landscape occupation between T2 and T3.

Occupancy matrices of species occurrence by landscape (i.e., 71 species \times 24 landscapes = 1704 possible occurrences) for each survey period provided insights into assemblage change over time. Region-wide decline in the occurrence of woodland birds between T1 and T2 (during drought) was substantial: 38% of species presences recorded in T1 were not recorded in T2 ($n = 270$ out of 718), and new records in T2 were rare ($n = 60$ colonizations; 12% of T2 species presence records). Some species recorded in T1, but not in T2, were observed back in the same landscapes in T3 (post-drought; e.g., Yellow-faced Honeyeater *Lichenostomus chrysops*; Grey Fantail *Rhipidura fuliginosa*); however, most were not (60%; e.g., Varied Sittella *Daphoenositta chrysoptera*, White-bellied Cuckoo-Shrike *Coracina papuensis*). Furthermore, ongoing losses were documented: 15% of species occurrences recorded in both T1 and T2 were absent in T3, and half of the T2 colonizations were not recorded in T3.

The NMDS ordination depicts the change in landscape bird assemblages over time (Fig. 1). Arrows showing the movement of individual landscapes in ordination space from T1 to T2 (Fig. 1a) reveal a similar and consistent direction (mean 58°) of change (Rayleigh $z_{0.69}$, $P < 0.01$). Similarly, landscapes showed consistent movement in the opposite direction (mean 237°) between T2 and T3 (Rayleigh $z_{0.74}$, $P < 0.01$; see arrows in Fig. 1b).

Region-wide change in bird assemblages

Bird assemblages in the study landscapes became more different from each other over time (differentiated) for both broad-sense (T1–T2, T1–T3) and turnover-related (all change-periods) measures of dissimilarity (Fig. 2). By contrast, the richness of landscape bird assemblages became more similar over time (homogenized: T2–T3, T1–T3).

Fig. 2 shows that each measure of assemblage composition (broad-sense, richness, turnover) exhibited a consistent pattern of either homogenization or differentiation over time. However the occupancy

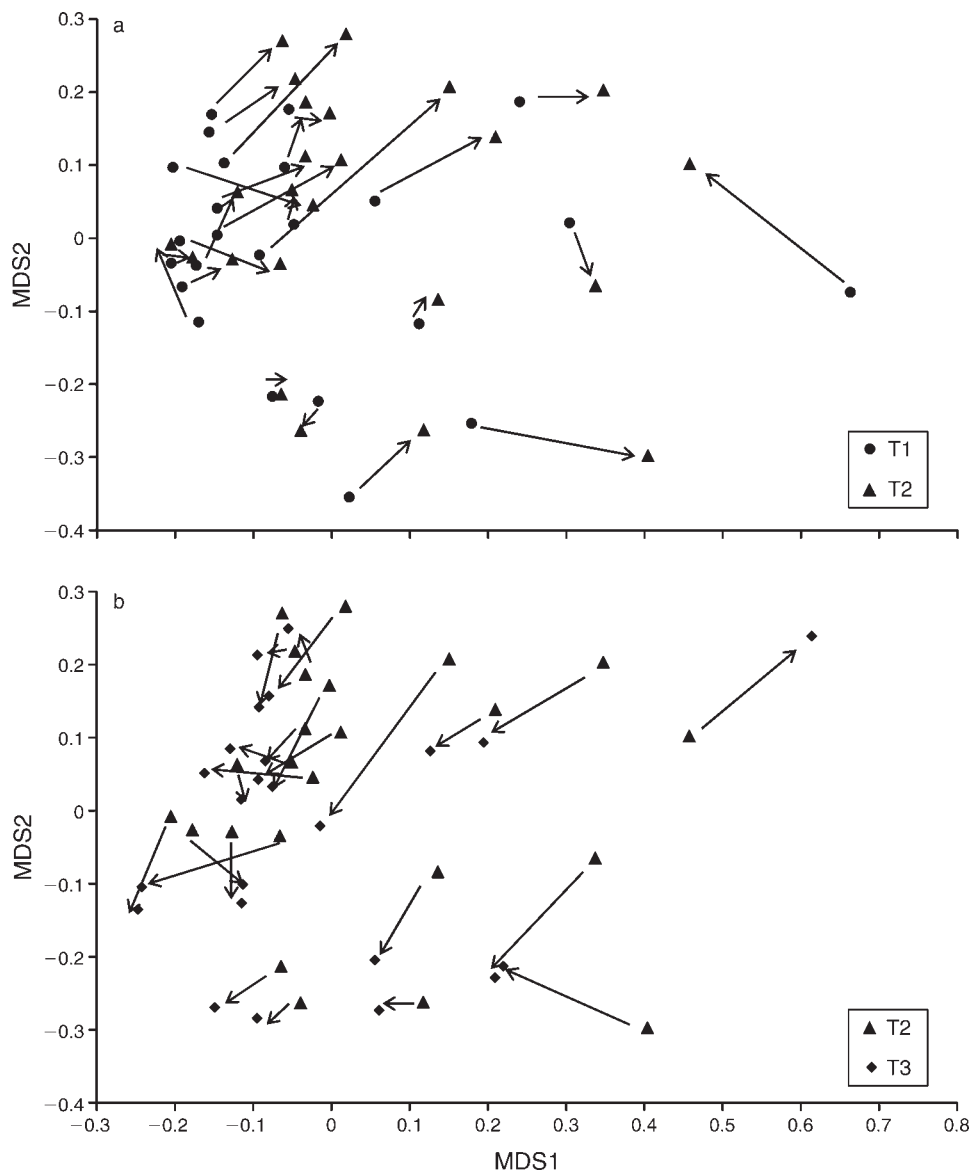


FIG. 1. Change in the composition of bird communities in study landscapes through time. Nonmetric multidimensional scaling ordinations of broad-sense dissimilarity indices representing bird assemblages ($n = 71$ species) in 24 landscapes and three survey periods (T1 = 2002–2003; T2 = 2006–2007; T3 = 2011–2012). Both (a) from T1 to T2 and (b) from T2 to T3 are based on identical and full data sets (i.e., including all three survey periods), but for simplicity the position of landscapes in T3 is not shown in (a) and the position of landscapes in T1 is not shown in (b). Arrows indicate the movement of individual landscapes over time.

matrices for each survey period suggest that the processes underlying these trends differed. For example, assemblages became more different from each other over time, in terms of the identity of species they comprised (i.e., turnover). Between T1 and T2, this was primarily due to a loss of species common to landscape pairs; between T2 and T3, this pattern was caused by the establishment of unique species in landscapes. In T3, many species ($n = 58$ out of 71; 82%) established in landscapes they had not occupied in T2; most of these ($n = 32$; 55%) established in only one or two landscapes, while only the Yellow-faced Honeyeater and Grey

Fantail established in more than 10 landscapes (11 and 12, respectively). Both processes (loss of common species, establishment of unique species) contributed to the pattern of turnover-related differentiation across the decade (T1–T3). Similarly, the increased similarity in the richness of assemblages, denoting a shortening of the richness gradient across landscapes, was driven by the addition of species to species-poor landscapes between T2 and T3, and the loss of species from richer landscapes between T1 and T3.

From T1 to T2, and across the overall decade (T1–T3), Mantel tests showed that changes in the identity of

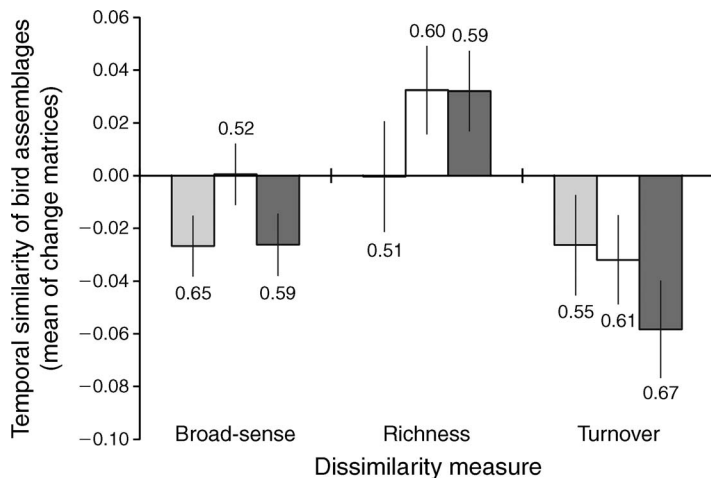


FIG. 2. Mean change in pairwise similarity of bird assemblages between landscapes over time (with 95% confidence intervals); positive values indicate homogenization, negative values indicate differentiation. Numbers above and below the bars indicate the proportion of all landscape-pairs showing that response (e.g., 65% of landscape-pairs showed broad-sense differentiation from T1–T2). Light gray indicates T1–T2; white indicates T2–T3; dark gray indicates T1–T3.

species (turnover) made the greatest contribution to broad-sense change (T1–T2; broad-sense \sim turnover Mantel $r = 0.44$; broad-sense \sim richness Mantel $r = 0.12$; T1–T3, broad-sense \sim turnover Mantel $r = 0.57$; broad-sense \sim richness Mantel $r = 0.08$). However, from T2–T3, Mantel tests showed that richness and turnover-related change had a similar influence on broad-sense change (both Mantel $r = 0.34$).

Landscape properties and temporal change in bird assemblages

There were some common patterns in the relative influence of landscape properties on the temporal dynamics in landscape bird assemblages (Fig. 3). These results are based on models containing all hypotheses with substantial support (i.e., included in models $\Delta_i \leq 4$ of the best) because no single best model was identified for any response variable (all $w_i < 0.9$; Appendix E). Broad-sense measures of assemblage dissimilarity for T1–T2 and T1–T3, here measuring change over time *within individual landscapes*, were influenced by habitat extent (TREE). The negative coefficients for TREE (Fig. 3a) indicate that bird assemblages changed most over time in landscapes with less native vegetation (Appendix F). The summed Akaike weights for this hypothesis in all change periods confirm the strong effect of habitat extent on broad-sense change (Appendix G). In addition, measures of landscape composition (VEGDIV) and context (SOURCE) also affected broad-sense change for T1–T3 (Fig. 3a). Broad-sense change across the decade was greatest in landscapes containing a lower diversity of native vegetation types, and located farther from large patches of native vegetation (Appendix F). Models explained 31–75% of the variation in broad-sense dissimilarity (Appendix E).

By contrast, variables representing landscape productivity had the strongest effect on richness and turnover-related change for T1–T2 and T2–T3 (Fig. 3b, c). Productivity measures had a negative effect on richness-related dissimilarity: that is, there was greatest

change in the richness of bird assemblages over time in *less* productive landscapes (less riparian vegetation, T1–T2/T2–T3; lower NDVI, T2–T3; Appendix F). By contrast, higher turnover in species identity over time occurred in *more* productive landscapes (higher NDVI) for T2–T3 (Appendix F). Relative to other landscape properties, productivity had a much stronger influence on richness-related change than on turnover-related change (Appendix G). Models for these relationships explained 39–66% of the variation in dissimilarity measures (Appendix E).

Over the full decade (T1–T3), measures of habitat extent and landscape composition and context had the strongest influence on turnover-related change. Higher turnover (change in species identity) was recorded in landscapes with less native vegetation, more grazing land, and those located farther away from large source areas (Fig. 3c, Appendix F). By contrast, change in richness over the full decade (T1–T3) was not strongly influenced by any landscape properties (Fig. 3b; Appendices E and G).

DISCUSSION

The frequency and magnitude of extreme climatic events, such as droughts, are predicted to increase with climate change (Easterling et al. 2000), yet there is a paucity of empirical data with which to assess their effects on biotic assemblages. Here, by using time-series data from multiple landscapes in southeastern Australia, we documented marked change in the composition of woodland bird assemblages in response to an extreme drought (van Dijk et al. 2013). These results corroborate patterns of change for individual bird species in this system (Mac Nally et al. 2009, Bennett et al. 2014b), and are consistent with drought having substantial effects on bird communities in other systems (Smith 1982, Albright et al. 2010).

We also show some recovery of the avifauna following drought-breaking rains, but full recovery of most individual species was not achieved by two years post-

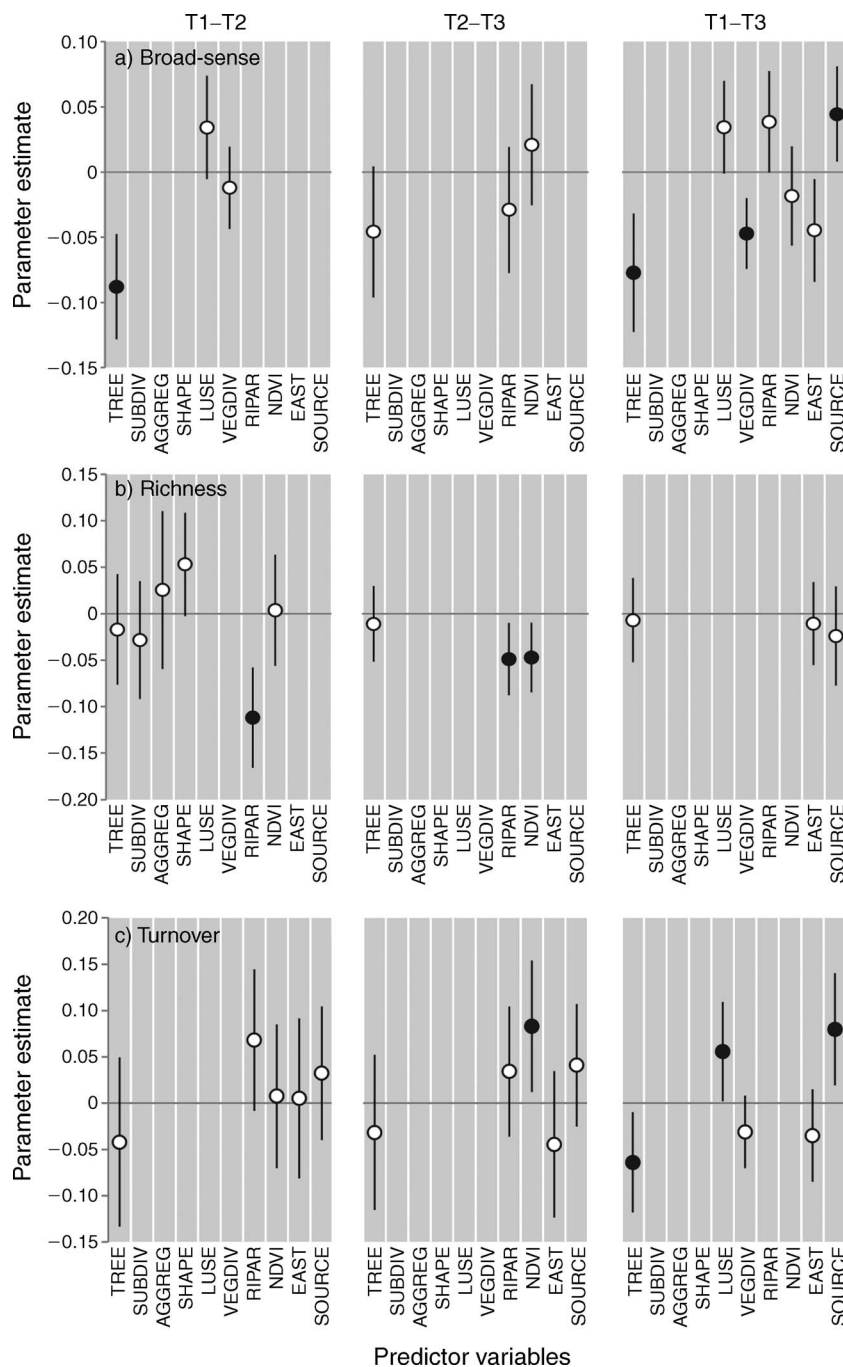


FIG. 3. Parameter estimates (with 95% confidence intervals) from models for the relationship between landscape properties and three measures of the dissimilarity of bird assemblages over time: (a) broad-sense dissimilarity, (b) richness-related dissimilarity, (c) turnover-related dissimilarity. Variables and hypotheses included in models are those represented in models with substantial support (i.e., Δ_i 4 of the best model). Each plot shows results for the change periods T1–T2, T2–T3, and T1–T3. Solid circles indicate parameter estimates for which the 95% confidence intervals do not include zero. For the predictor variables, see *Methods: Landscape properties*.

drought (Bennett et al. 2014b). While future sampling may reveal additional recovery, partial recovery is consistent with other research: at 2–3 years post-drought, plant richness in North American grasslands remained diminished (Tilman and Haddi 1992), and a

UK study found two-thirds of butterfly populations were below pre-drought levels (Oliver et al. 2013). Such results relate to annual drought events, whereas we have examined the effects of nine years of drought (van Dijk et al. 2013), which may require much longer recovery

time. Post-drought recovery of birds may also exhibit time lags due to slow rates of recovery in habitat features, such as shrub cover (Bennett et al. 2013) and eucalypt flowering, and/or slow reproductive rates of individual species. Alternatively, the lack of full recovery identified here may also reflect an ongoing decline in woodland birds, consistent with the notion of an extinction debt (Tilman et al. 1994), potentially further compounded by drought.

Region-wide change in bird assemblages over severe drought

By partitioning compositional change into components associated with change in richness vs. that associated with turnover in the identity of species (Carvalho et al. 2012), our analyses provide new insights into the role of drought in structuring woodland bird assemblages across this region. The turnover component of compositional change consistently indicated a differentiation of assemblages through time, whereas the richness-related component indicated homogenization, particularly during recovery from drought (T2–T3). However, change in species identity (turnover) contributed most strongly to the overall compositional change (broad-sense change) across the study, such that the net effect of the drought period is one of increased differentiation of the woodland bird assemblages among landscapes.

Although turnover-related differentiation was recorded for change periods corresponding to drought and post-drought recovery, these patterns were caused by different types of change. During drought, the main cause of differentiation was a loss of species from landscapes, whereas a gain of a unique collection of species for each landscape was more influential during recovery from drought. Examination of the raw data indicates the same species often contributed to both trends, as several species (e.g., Horsfield's Bronze-Cuckoo *Chrysococcyx basalis*, White-winged Triller *Lalage sueurii*) were lost from, then gained by, many landscapes during and after drought, respectively. Thus, while our results reveal clear temporal dynamics in woodland bird assemblages in response to climatic disturbance, they do not suggest wholesale reshuffling of communities, as has been identified for desert rodents (in response to flood [Thibault and Brown 2008]).

Over the full decade, we recorded a contraction of the richness gradient of bird assemblages across landscapes, caused by a disproportionate loss of species from species-rich landscapes. As the richness-related homogenization recorded during post-drought recovery (T2–T3) was due to a different process (the addition of species to species-poor landscapes), the loss of species from richer landscapes appears to reflect more gradual, longer-term trends occurring in the region. When considered in light of other results from the same region, showing incomplete recovery of the avifauna after the Millennium drought and ongoing declines in

species' reporting rates (Bennett et al. 2014b), these findings have implications that should cause concern for woodland bird conservation.

Landscape properties affect change in bird assemblages over severe drought

Our study design, based on measuring temporal changes in a series of landscapes that represent a steep gradient in landscape modification, provided a unique opportunity to examine the interaction between drought and anthropogenic land use. A key finding was that compositional changes in woodland bird assemblages differed between landscapes, and that these differences occurred in a predictable way that was related to measured properties of the study landscapes.

The total amount of native wooded vegetation in the landscape had a consistently strong effect on overall (broad-sense) change in the composition of landscape bird assemblages over time. Measures of habitat cover are known to be a dominant influence on static patterns in the occurrence of individual species (Trzcinski et al. 1999, Mortelliti et al. 2010), and in the richness of woodland birds (Radford et al. 2005) at the landscape scale. Very little is known about the relationship between landscape properties and assemblage composition in whole landscapes (but see Dormann et al. 2007). Here, assemblages in landscapes with more native vegetation were more stable both during an extreme climatic event (T1–T2), and across the full decade. Oliver et al. (2013) similarly identified increased resistance (lower declines) of butterfly populations to a drought event at sites with more surrounding habitat. Such findings are underpinned by theoretical understanding of the positive relationship between habitat area and population size, with larger populations being less vulnerable to the effects of stochastic disturbances such as drought events (McLaughlin et al. 2002, Piessens et al. 2009). Results also emphasized the importance of extensive areas of native wooded vegetation for maintaining more stable bird assemblages in the longer term, by potentially providing source populations for dispersal and recolonization.

The important influence of landscape productivity on assemblage dynamics in response to drought was revealed by partitioning compositional change into the component processes of richness- and turnover-related change (Carvalho et al. 2012). Landscapes with higher natural productivity showed less change in the richness of associated assemblages, yet exhibited higher turnover in the identity of bird species over time. Riparian vegetation, one measure of landscape productivity, is well recognized as a critical habitat that supports diverse biotic assemblages (Sabo et al. 2005), and can increase habitat connectivity (Naiman et al. 1993) and provide refuge habitat for a range of species during drought (Seabrook et al. 2011). Furthermore, riparian vegetation makes a disproportionate contribution, relative to non-riparian vegetation, to avifaunal diversity in modified

landscapes in this system (Bennett et al. 2014a). The current findings add a novel, temporal perspective to the importance of riparian vegetation. The increased turnover recorded in more productive landscapes in T2–T3 suggests higher species replacement. However, such dynamics were not at the expense of community richness, as such landscapes also showed increased stability in terms of the richness-related component of compositional change.

CONCLUSIONS

Extreme climatic events are predicted to increase in magnitude and frequency with climate change (Easterling et al. 2000), and pose an additional challenge to understanding the status and future trajectory of biota in anthropogenic environments. Here, severe drought resulted in marked shifts in the composition of woodland bird assemblages in rural landscapes. Notably, assemblages did not become more homogenized among landscapes, but rather became more distinct over time, primarily due to a turnover-related differentiation in the avifauna. Compositional change differed between landscapes in a predictable way, which reflected different patterns of removal of native vegetation that occur in different landscapes. Overall, landscapes that retained a greater amount of native woody vegetation had more stable bird assemblages; landscapes depleted of native vegetation experienced greater turnover of species over severe drought. Further, the amount of vegetation in productive parts of the landscape, such as riparian woodland, had stronger effects on richness-related change, yet more productive landscapes are under the greatest pressure for agricultural clearing. It is not possible to prevent extreme climatic events, but our results highlight a capacity to mediate the effects of severe drought on woodland birds by managing rural landscapes to retain large extents of native vegetation cover, particularly that in productive areas such as along streams and floodplains. These directions are consistent with broader goals for ecological restoration in rural landscapes (Lindenmayer and Fischer 2006), and will have wider benefits in terms of aesthetic quality, maintenance of ecological processes, and provision of ecosystem services (Naiman et al. 1993).

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–G are available online: <http://dx.doi.org/10.1890/14-2447.1.sm>