

Do state-and-transition models derived from vegetation succession also represent avian succession in restored mine pits?

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Abstract. State-and-transition models are increasingly used as a tool to inform management of post-disturbance succession and effective conservation of biodiversity in production landscapes. However, if they are to do this effectively, they need to represent faunal, as well as vegetation, succession. We assessed the congruence between vegetation and avian succession by sampling avian communities in each state of a state-and-transition model used to inform management of post-mining restoration in a production landscape in southwestern Australia. While avian communities differed significantly among states classified as on a desirable successional pathway, they did not differ between desirable and deviated states of the same post-mining age. Overall, we concluded there was poor congruence between vegetation and avian succession in this state-and-transition model. We identified four factors that likely contributed to this lack of congruence, which were that long-term monitoring of succession in restored mine pits was not used to update and improve models, states were not defined based on ecological processes and thresholds, states were not defined by criteria that were important in structuring the avian community, and states were not based on criteria that related to values in the reference community. We believe that consideration of these four factors in the development of state-and-transition models should improve their ability to accurately represent faunal, as well as vegetation, succession. Developing state-and-transition models that better incorporate patterns of faunal succession should improve the ability to manage post-disturbance succession across a range of ecosystems for biodiversity conservation.

Key words: *bird communities; conservation; deviated states; disturbance; jarrah, Eucalyptus marginata; management; mining; production landscape; restoration; southwestern Australia; state-and-transition model; succession.*

INTRODUCTION

Management of biodiversity in production landscapes is typically a process of managing natural and anthropogenic disturbance regimes and post-disturbance succession (e.g., Spring et al. 2008, Souza et al. 2012). Given the plurality of land uses often practiced in production landscapes, biodiversity conservation in these landscapes often involves the management of both natural disturbances, such as fire or drought, and anthropogenic disturbances, such as logging or mining (Havel 1989, Stockmann et al. 2010, Walker 2011). The effect of disturbances on biodiversity is dependent on both the spatial extent and severity of the disturbance (Fraver et al. 2009, Lindenmayer et al. 2014) and, if the disturbance is severe enough, then management may need to actively intervene to assist post-disturbance ecosystem recovery.

One active intervention that is often used in production landscapes after particularly severe disturbances, such as mining, is restoration (Cristescu et al. 2012, Wassenaar et al. 2013). However, if restoration is to effectively contribute to conserving biodiversity in production landscapes, it will need to effectively restore both flora and fauna. Furthermore, restored areas will need to follow desirable successional pathways post-disturbance and end up at a desired endpoint, or range of endpoints, that contribute long term toward the maintenance of biodiversity in those landscapes (Prach and Walker 2011). Ecologically, restoration is simply a process of managing succession post-disturbance (SERI 2004) and, therefore, succession needs to be conceptualized, understood, and managed toward a desired endpoint or range of endpoints (e.g., Koch and Hobbs 2007, Woodcock et al. 2011).

Currently, there are three main ecological models that conceptualize how succession proceeds within any given area: the deterministic, stochastic, and alternative stable states models (Hobbs et al. 2007). The deterministic model states that succession in restored areas will

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proceed along a predetermined pathway toward a stable climax community (Odum 1969). In this model, management input would be low or none, as the endpoint would be achieved regardless, although management can serve to accelerate some successional processes. In the stochastic model, succession in restored areas could proceed along an infinite number of pathways to a dynamic endpoint (Kreyling et al. 2011). In this model, management would be very difficult as it would be unclear whether management inputs would necessarily drive systems toward any potential endpoint. The third model, the alternative stable states model, states that succession in restored areas can proceed along one of several possible predetermined trajectories (Zweig and Kitchens 2009), the trajectory determined by a range of both abiotic and biotic factors (see, e.g., Wong et al. 2010). Based on this model, management input in restored areas would be variable. If succession proceeded along desirable pathways, little management input would be required but, if any deviations from desirable successional pathways were detected, then management interventions would be required to drive succession back onto a desirable pathway (Hobbs and Norton 1996). This model recognizes that systems are dynamic and can proceed along a number of successional pathways, but also recognizes that there are ecological limits to the number of pathways.

The concept of alternative stable states is often conceptualized in state-and-transition models, which were originally developed to describe dynamic processes in ecosystems (Westoby et al. 1989) but lend themselves well to describing successional processes. In a successional context, these models state that, along multiple successional pathways, there are alternative semi-stable ecological states that can exist (Schmitz et al. 2006). Transitions between these semi-stable states are often rapid and can be caused by a range of factors, including disturbances and altered management regimes (Santana et al. 2010). These models have recently gained favor in conceptualizing succession (e.g., Hobbs and Suding 2009), partly as they are applicable across many ecosystems. This is because, while these states are necessarily an abstraction that encompass a certain amount of variation in space and time, they are still a very useful method for summarizing knowledge about dynamic successional processes, even in systems where states are not clearly demarcated and transitions may be progressive (Mayer and Rietkerk 2004). Another factor in their popularity is that these models lend themselves very well to conceptual frameworks for management (Bestelmeyer et al. 2004, Knapp et al. 2011). This is because transitions are often caused by altered management regimes, which implicitly assumes that specific management regimes can be used to drive ecosystems into specific states (Bestelmeyer et al. 2011).

There is increasing evidence that many restored areas require long-term management if they are to proceed along a successional pathway and arrive within a range

of end points that benefit biodiversity, presumably through resembling the reference community (Craig et al. 2010, Woodcock et al. 2011, Craig et al. 2012). Given this need for management, it is unsurprising that state-and-transition models are increasingly used in the management of restored areas (e.g., Smith et al. 2003). However, these state-and-transition models have been primarily based on vegetation succession and, as far as we are aware, there has been no evaluation of whether these models are also appropriate for describing faunal succession in restored areas. While the distribution and abundance of fauna is fundamentally affected by the structure and floristics of habitats (e.g., Jayapal et al. 2009, Uezu and Metzger 2011; hence, we define faunal succession as changes in faunal composition and abundance with changes in vegetation structure and floristics), state-and-transition models will only capture that congruence if they are based around structural and floristic variables that are important drivers of faunal community composition. Given the importance of fauna in a range of ecosystem processes (e.g., Allen-Wardell et al. 1998, Dixon 2009), it is important that management ensures that faunal succession is also proceeding along a desirable pathway, if restored areas are to end within the range of desired end points.

Alcoa of Australia has mined and rehabilitated over 13 000 ha in the northern jarrah (*Eucalyptus marginata*) forest of Western Australia (Koch 2007a). The restoration is managed for a range of uses, including timber, water catchment, and biodiversity conservation (Grant and Koch 2007). To ensure that restoration contributes toward these multiple objectives, a series of completion criteria have been developed and management actions conducted to ensure that these completion criteria are met (Grant and Koch 2007). To conceptualize when and which management actions are required, a state-and-transition model was developed by Grant (2006) that identified a series of desirable states that did not require management and a series of deviated states that required management inputs to drive them back onto a desirable successional pathway. In this model, desirable states represented different stages of vegetation succession and deviated states were separated from desirable states of the same restoration age based on eucalypt and legume stem densities (Grant 2006). However, the utility of this model for managing faunal succession is unclear. To assess the utility of the model for managing faunal succession, we examined avian communities in each of the states found in Grant's (2006) state-and-transition model and evaluated the congruence between avian and vegetation succession. We asked the following questions: (1) Do various successional states on a desirable trajectory represent different avian communities and can further additional successional states be identified?; (2) Do avian communities in deviated states differ from desirable states of the same age?; and (3) If there is no congruence between state-and-transition models for vegetation and avian succession, why do they differ?

METHODS

Study area

The study was conducted at Alcoa of Australia's Huntly Mine (32°36' S, 116°06' E), 15 km NNE of Dwellingup in southwest Western Australia. The climate at Dwellingup is Mediterranean with hot, dry summers and cool, wet winters. Average rainfall is 1236 mm/yr with over 75% falling between May and September. The original vegetation at Huntly consisted of jarrah forest, a dry sclerophyll forest with the canopy consisting almost entirely of two eucalypts, jarrah, and marri (*Corymbia calophylla*). *Banksia grandis* is a typical midstory species, and typical understory species are *Acacia lateriticola*, *Bossiaea aquifolium*, *Lasiopetalum floribundum*, *Tetraria capillaris*, and *Xanthorrhoea preissii*. Following mining, the mine site consists of a mosaic of unmined jarrah forest and restored mine pits of varying ages. Current restoration practices, used since 1988, involve reseedling with *E. marginata* and *C. calophylla* and 76–111 local understory species, and hand planting of recalcitrant species that do not return from seed (Koch 2007b). Restored mine sites have similar plant species compositions to unmined jarrah forest, although dryland rush and sedge species are less common. For further details of mining and restoration procedures used, see Grant and Koch (2007) and Koch (2007a).

Study design

Grant (2006) aimed to present a state-and-transition successional model (hereafter Grant's STM) that focused on identified completion criteria, defined as restoration performance objectives, and assessed the usefulness of this model in describing the succession of restored areas in the jarrah forest of Western Australia. Critically, the model also aimed to identify sites that did not meet existing completion criteria and proposed management manipulations designed to ensure these sites would satisfy the completion criteria (Grant 2006). We used Grant's STM to identify the five desirable and five deviated states existing on Alcoa's mining lease (see Fig. 6 in Grant 2006). From the five desirable states, we eliminated active mine pits (S0; terminology from Grant 2006) and recently ripped pits (S1) as these lacked vegetation and so, we assumed, birds as well. Of the remaining desirable states, we included 0–5 yr old restoration (S2) and unmined jarrah forest (Sx). As 5-yr-old restoration is very different structurally to 15-yr-old restoration (Norman et al. 2006, Craig et al. 2012), we investigated whether existing states could be divided further by dividing 5- to 15-yr-old restoration (S3) into 5- to 10- (S3a) and 10- to 15-yr-old (S3b) restoration. Since the publication of Grant's STM, some older mine pits have been re-incorporated into state-managed control burning regimes, and so we also included postburn mine pits (S5), although no mine pits were identified as being in this state in Grant (2006). This

gave us a total of five desirable states, including the unmined forest reference sites (Sx; Fig. 1). Of the five deviated states, two (D4 and D5) occupied parts of mine pits that were smaller than proposed bird sampling methods and so were eliminated, leaving us with three deviated states to sample: 0–5 yr old restoration with sparse legumes (D2); 5–10 yr old restoration with overdense eucalypts (D3); and 10–15 yr old restoration with overdense eucalypts (D7; Fig. 1).

For each of these eight states, we tried to minimize the range of restoration ages within each state and kept the range of ages narrower in young restoration than in old restoration because restoration changes less rapidly from year to year as it matures (Norman et al. 2006). We chose the range of restoration ages that gave us the greatest sample sizes for each state, while also enabling us to contrast deviated states against desirable states of exactly the same post-mining age. Consequently, we ended up with desirable and sparse 1–2 yr old restoration (S2 and D2), desirable and overdense 6–7 yr old restoration (S3a and D3), desirable and overdense 11–13 yr old restoration (S3b and D7), 16–18 yr old postburn restoration (S5), and unmined forest (Sx). Within these states, chosen mine pits were a minimum of 5 ha in area so that bird sampling points could be established at a minimum of 80 m from mine pit edges to minimize edge effects (see *Methods: Bird sampling*), which resulted in seven mine pits in each state for bird sampling, except for 1–2 yr old restoration with sparse legumes (D2), where only five mine pits were available.

Bird sampling

As the vegetation in many mine pits was very dense, we sampled birds using 40 m fixed-radius point counts. A 40 m radius was the maximum radius in which we felt confident of detecting most birds within the count area, and an examination of detectability profiles for common species in Distance 6.0 (Thomas et al. 2010) confirmed that this was the most appropriate radius at which to truncate observations. Each site contained two point count stations located 100 m apart to provide adequate spatial sampling of each site, and each station was a minimum of 80 m from either unmined forest or other mine pits to minimize edge effects. We concluded that edge effects did not have a strong influence on the bird communities we sampled in mine pits because, even in rainforests, most edge effects occur within 40 m of an edge (Murcia 1995, Laurance et al. 2002), edge effects in the open jarrah forest are not marked (Craig 2007, Craig et al. 2015), and bird communities in mine pits are quite different from those in unmined forest (see *Results*). While bird communities sampled in mine pits undoubtedly contained some rare species with large home ranges that encompassed adjacent habitats (see *Discussion*), <2% of the area of mine pits is >120 m from unmined forest or mine pits of a different age, so our sampling regime, regardless of edge effects, would have sampled

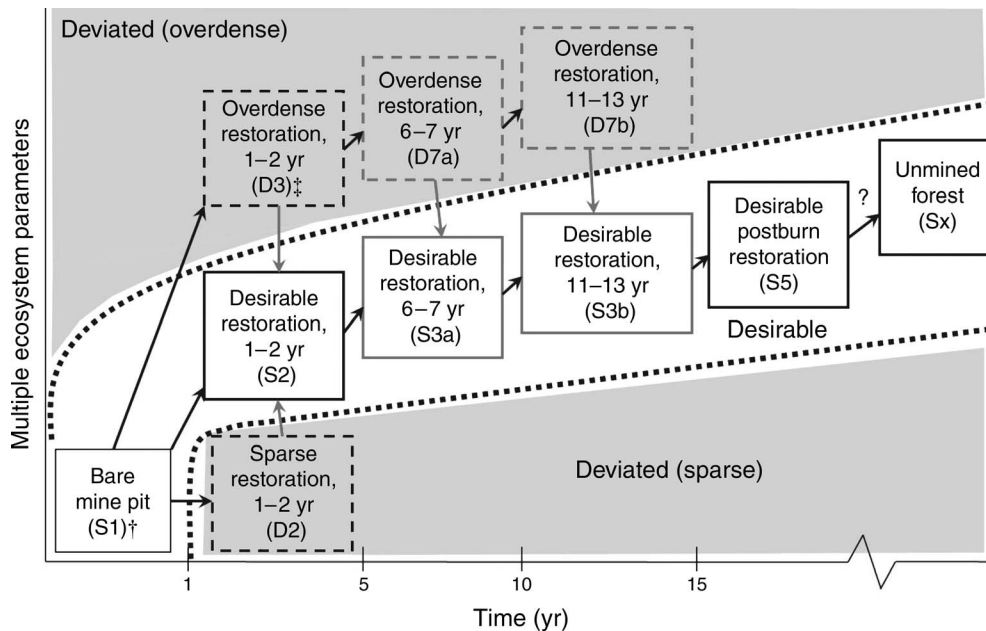


FIG. 1. Conceptual state-and-transition model of succession in restored bauxite mine pits in the jarrah forest of Western Australia. States on a desirable trajectory are shown on a white background, while states in a deviated state are shown on a gray background. States outlined in black are present in Grant (2006), whereas states outlined in gray are additional states investigated in this study. States outlined in dashed lines represent states outside the desirable trajectory, while states outlined in solid lines represent states within the desirable trajectory. Black arrows represent ecological succession and gray arrows represent potential management actions. Numbers in parentheses refer to the designation of states from Grant (2006). The † symbol indicates the state was not included in our study due to the lack of birds; the ‡ indicates the state was not included in our study as succession had progressed and no pits existed in this state.

the bird communities typical of mine pits in each particular state.

Each station was sampled once each in late winter (24 August–13 September 2008), early spring (14 September–4 October 2008), mid-spring (5 October–25 October 2008) coinciding with the main breeding season in the study area, giving a total of eight point counts conducted at each site. During each point count, the distance from the station to all birds seen or heard within 40 m of the station was recorded. Birds flying over plots were only included if they were using the habitat (i.e., foraging artamids, hirundinids, and raptors). All point counts were conducted within five hours of sunrise, in light winds (<20 km/h) with no rain, and the order in which pits were sampled was randomized with respect to time since sunrise. All point counts were conducted by M. D. Craig to eliminate observer bias.

Vegetation sampling

At each point count station, we estimated vegetation structure along transects that originated at the stations themselves. The first transect direction was chosen at random, then the remaining two transects were run 120° to either side, and we estimated vegetation structure 10 m and 30 m from the point count station along these three transects. At each point, we visually estimated litter cover, bare ground, and overall vegetation cover in

three strata (0–1, 1–2, and 2–5 m, respectively) in 0.25-m² plots. We estimated canopy cover, using a densitometer, in each of the four compass directions and averaged these to estimate canopy cover at each point. From each point, we measured distances to the nearest understory plant (0.6–3 m in height), overstory plant (>3 m in height), legume and eucalypt (no height restriction for either), and used these distances to calculate densities of these four variables using the formula from Barbour et al. (1987). We used a clinometer to estimate heights of the three tallest trees visible from each point count station and averaged these to estimate canopy height. Finally, we measured the length and diameter at both ends of all coarse woody debris (CWD; defined as >10 cm at largest end) on 5 × 5 m plots centered on each point and used these to calculate the volume of CWD (m³/ha). All data from the two stations were averaged to provide a single value for each mine pit or unmined forest site.

Statistical analysis

We first examined whether vegetation structure differed significantly among the five desirable states (1–2, 6–7, 11–13, and postburn restoration and unmined forest) by normalizing variables and then creating a between-site resemblance matrix using a Euclidean similarity measure. We then used this resemblance matrix to visually represent the data using a principal

coordinates analysis (PCO) and examine differences among the five states using a one-factor permutational multivariate analysis of variance (PERMANOVA) with pairwise comparisons if significant differences existed. To determine which structural variables differed significantly among the five desirable states, we first tested for heteroscedascity using a Levene's test and transformed variable using $\ln(x + 1)$ where required. We then conducted ANOVAs with each structural variable as the dependent variables and state as the independent variable and used a least significant difference test (LSD) to examine pairwise differences when state effects were significant (Day and Quinn 1989).

We determined whether vegetation structure differed between desirable and deviated restored states of the same age by analyzing each restoration age separately. For each of the three data sets (desirable and sparse 1–2 yr old restored sites; desirable and overdense 6–7 yr old restored sites; and desirable and overdense 11–13 yr old restored sites), we normalized variables and then constructed between-site resemblance matrices using a Euclidean similarity measure. We then used this resemblance matrix to visually represent the data using PCO and examine differences between states using a one-factor PERMANOVA. For these analyses we excluded cover from 2 to 5 m, canopy cover and overstory density from 1–2 yr old sites, and CWD volume from 11–13 yr old sites because all sites had zero values for these variables. To determine whether structural variables differed significantly between desirable and deviated states of the same age, we first tested for heteroscedascity using a Levene's test and transformed variables using $\ln(x + 1)$ where required. We then conducted independent t tests with each structural variable as the dependent variable and each state (desirable or deviated) as the grouping variable.

To determine whether avian communities differed significantly among desirable states, we first standardized all bird species to the same relative abundance unit, while accounting for detectability differences among states for those species where we obtained insufficient detections to determine detectability profiles. To achieve this, we transformed all data to the number of point counts, out of a possible total of eight point counts at each site, when a species was detected and then used this detection rate to create a between-site resemblance matrix using a Bray-Curtis similarity measure. We then used this resemblance matrix to visually represent the data using a PCO, examine differences among the five states using a one-factor PERMANOVA, with pairwise comparisons if significant differences existed, and conduct a distance-based linear model (DISTLM) to identify which vegetation structural characteristics showed significant relationships with the overall avian community, after removing highly correlated variables (litter cover, bare ground, and canopy cover were all highly correlated ($r_{31} > 0.9$), so only litter cover was retained). We analyzed whether the community metrics,

overall bird abundance (birds/ha), and bird species richness (species/site), differed among desirable states using ANOVAs with the community metrics as the dependent variables and desirable states as the independent variables, and identified which states were causing any significant difference using LSD (Day and Quinn 1989). For overall bird abundance, we used Distance 6.0 (Thomas et al. 2010) to derive detection profiles to correct for detectability differences among desirable states. To analyze individual species, we first divided all bird species up into three groups: common species (>60 detections), frequent species (20–60 detections), and uncommon species (5–19 detections). For common species, we corrected for detectability differences among desirable states as we did for overall bird abundance. For frequent species, we corrected for detectability by converting relative abundance to a detection rate as we did for avian communities. For uncommon species, we also used detection rates but only analyzed those species where $>50\%$ of detections were in a single treatment.

To examine whether avian communities differed significantly between desirable and deviated restored states of the same age, we again divided the data into three sets, based on restoration age as we did for vegetation structure, and analyzed them separately. Neither vegetation structure (see *Results*) nor avian detection profiles differed between desirable and deviated states of the same restoration age, precluding the need to correct for detectability. Hence, we used uncorrected data (individuals/site) to create between-site resemblance matrices using a Bray-Curtis similarity measure and conducted PERMANOVAs on these matrices to determine whether the avian communities differed between desirable and deviated states of the same restoration age. Before determining whether the community metrics, overall bird abundance (individuals/site) and species richness (species/site), and individual species differed significantly between desirable and deviated states of the same age, we tested for heteroscedascity using a Levene's test and transformed variables using $\ln(x + 1)$ where required. We then conducted independent t tests with either the community metric or individual species relative abundance as the dependent variable and state (desirable or deviated) as the independent variable. We restricted the analyses on individual species to those species recorded ≥ 5 times.

As there were no differences in avian communities, and only a single difference in the abundance of any species, between desirable and deviated plots (see *Results*), we combined data from all desirable and deviated plots and unmined forest to examine bird-vegetation relationships. Before commencing analyses, we found that both bare ground and canopy cover were highly correlated with litter cover (both $r_{52} > 0.9$), so we retained only litter cover. We explored relationships between habitat structure and avian community metrics or bird species abundances using best subset modeling with bird variables as the dependent variables and the 11

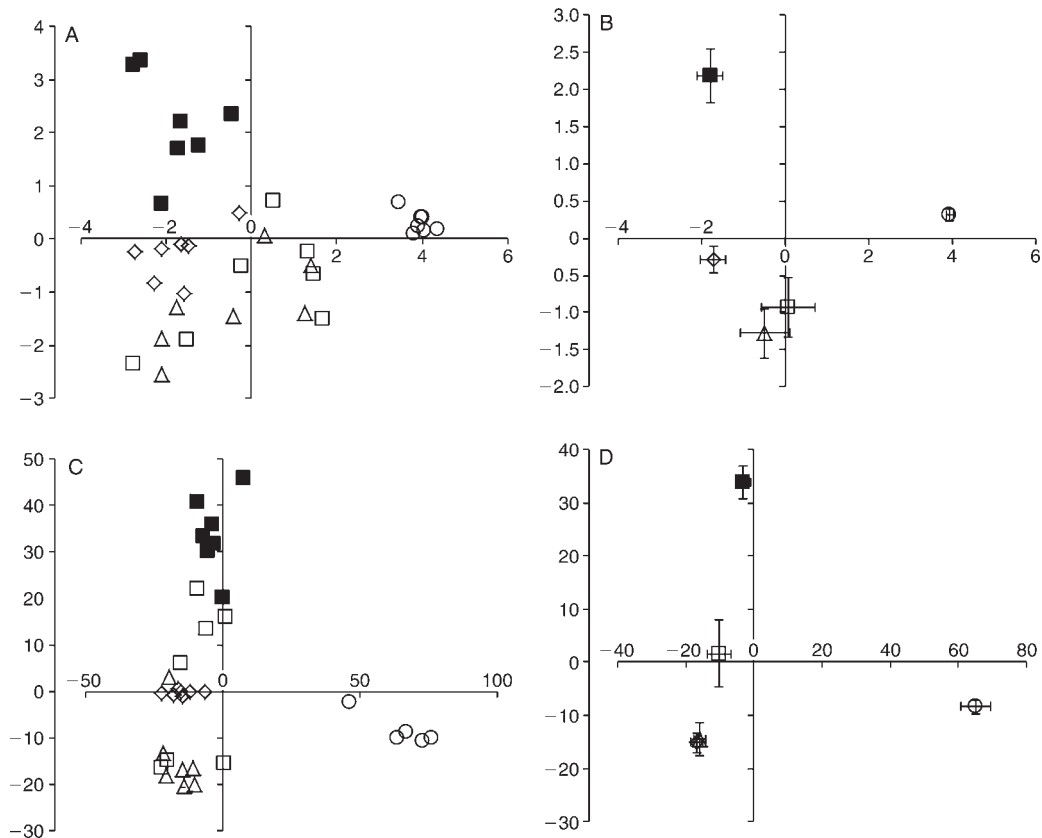


FIG. 2. Principle coordinate analyses (PCOs) of (A, B) vegetation structure and (C, D) bird communities in desirable 1–2 yr old (open circle), 6–7 yr old (triangle), 11–13 yr old (diamond), and 16–18 yr old postburn restoration (open square), as well as unmined forest (solid square), showing all sites (A, C) and centroids of each state (B, D). Error bars show \pm SE.

structural variables as the predictor variables. We used generalized linear models with a gaussian distribution and an identity link function to model all possible subsets of the predictor variables. We ranked all models using Akaike's information criterion corrected for small sample sizes (AIC_c) and calculated the weight (ω_i) of each model, which is the probability that that model is the best model. We considered all models with a ΔAIC_c (difference in AIC_c value between models) of <2 from the best model to be plausible and considered all models with a $\omega_i > 0.1$ to be well supported (Burnham and Anderson 2002). However, as no models were well supported (see *Results*), we further explored relationships between habitat structure and avian community metrics and bird species abundances using multimodel inference based on the entire set of models using model weights. Weights were summed for all models containing that predictor variable, which was the same number of models for each variable, and the predictor variable with the largest predictor weight was estimated to be the most important, while the variable with the smallest sum was estimated to be the least important predictor (Burnham and Anderson 2002). Then, by using the weighted average for that parameter across models (e.g., standardized regression coefficient) inference was based on

the entire set of models. This approach has both practical and philosophical advantages, as it is based on the Kullback-Leibler information theory. A model-averaged estimator has a more honest measure of precision and reduced bias compared to the estimator from just the selected best model (Burnham and Anderson 2004). We considered all variables with summed model weights >0.4 to be well supported (Converse et al. 2006).

RESULTS

Vegetation differences among states

Differences in vegetation structure among desirable states.—Overall vegetation structure differed significantly among desirable states (pseudo- $F_{4,30} = 10.67$, $P < 0.001$) and all states were significantly different from one another ($t_{1,12} > 1.80$, $P \leq 0.008$) except 6–7 yr old and 16–18 yr old postburn restoration ($t_{1,12} = 1.39$, $P = 0.090$; Fig. 2). All structural variables differed significantly among desirable states (see Appendix A) and variables differed in their successional patterns. Cover from 0 to 1 m, canopy cover, and understory density all increased significantly from the 1–2 yr old to the 6–7 yr old restoration but then did not change significantly

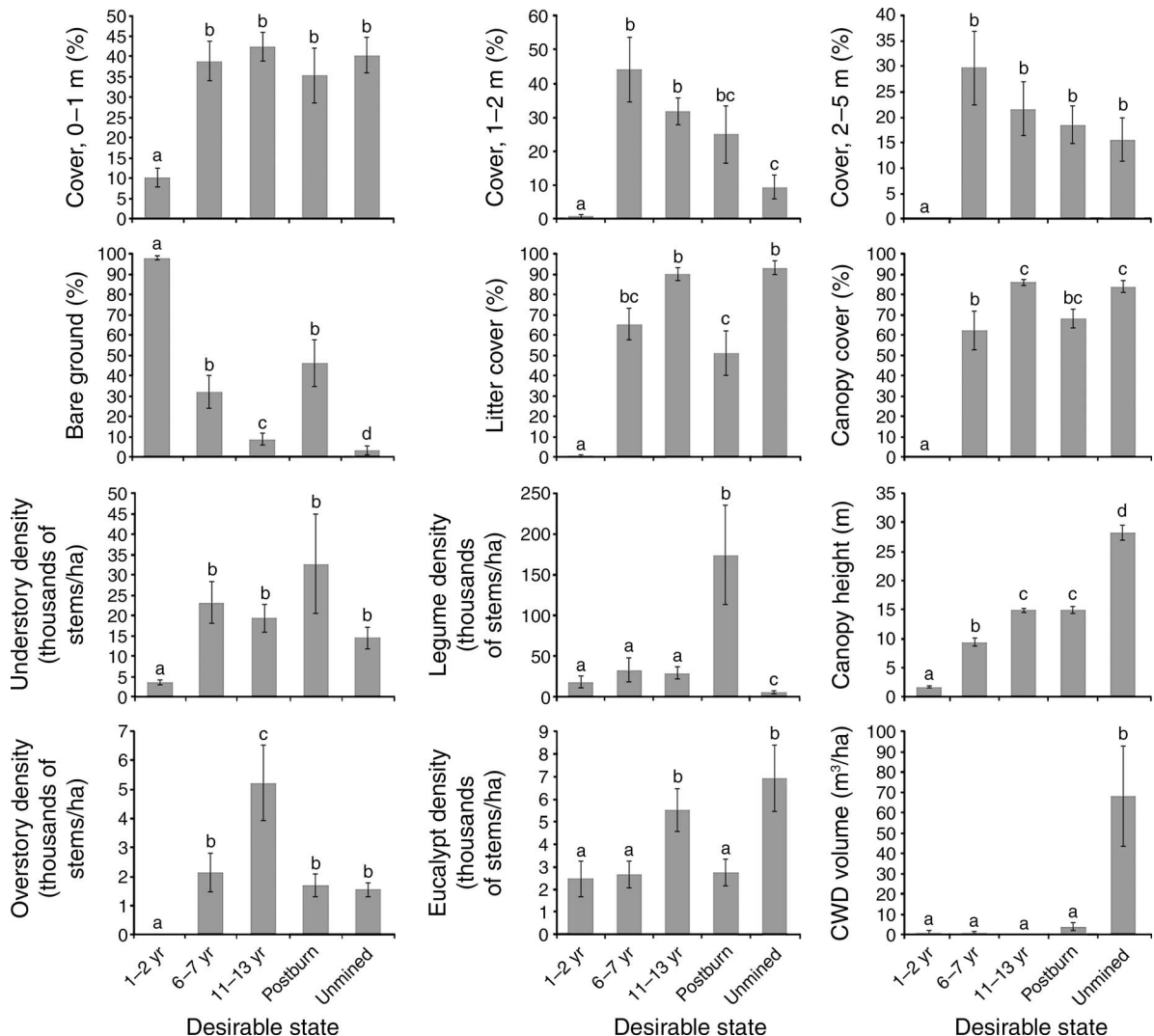


FIG. 3. The 12 measured structural variables (mean \pm SE) showing successional patterns as restoration ages plus differences between restoration and unmined forest. Letters above the error bars denote means that are significantly different ($P < 0.05$). CWD is coarse woody debris.

(Fig. 3). CWD volume was significantly greater in unmined forest than any restoration age, while successional patterns in the remaining variables were more complex (Fig. 3).

Differences in vegetation structure between deviated states and desirable states of the same age.—Overall vegetation structure did not differ between desirable and sparse 1-2 yr old (pseudo- $F_{1,12} = 0.80$, $P = 0.658$), desirable and overdense 6-7 yr old (pseudo- $F_{1,12} = 1.16$, $P = 0.297$) or desirable and overdense 11-13 yr old restoration (pseudo- $F_{1,12} = 2.24$, $P = 0.052$; Fig. 4). No individual variables varied between desirable and sparse 1-2 yr old restoration ($t_{10} \leq 1.60$, $P \geq 0.141$; see Appendix A). There was significantly more bare ground in overdense 6-7 yr old restoration, compared to desirable restoration ($55\% \pm 6\%$ vs. $32\% \pm 8\%$, mean

\pm SE; $t_{12} = -2.26$, $P = 0.043$), but none of the remaining variables differed significantly ($t_{12} \leq 2.12$, $P \geq 0.056$; Appendix A). Desirable 11-13 yr old restoration had more canopy cover (86 ± 2 vs. $73 \pm 4\%$ [mean \pm SE]; $t_{12} = 3.02$, $P = 0.011$) and taller canopies (14.9 ± 0.3 vs. 12.9 ± 0.6 m, mean \pm SE; $t_{12} = 2.89$, $P = 0.013$) than overdense 11-13 yr old restoration, but none of the remaining variables differed significantly ($t_{12} \leq 1.64$, $P \geq 0.128$; Appendix A).

Do various successional states on a desirable trajectory represent different avian communities and can further additional successional states be identified?

Avian communities differed significantly among desirable states (pseudo- $F_{4,28} = 8.35$, $P < 0.001$). Avian communities in 1-2 yr old restoration were significantly

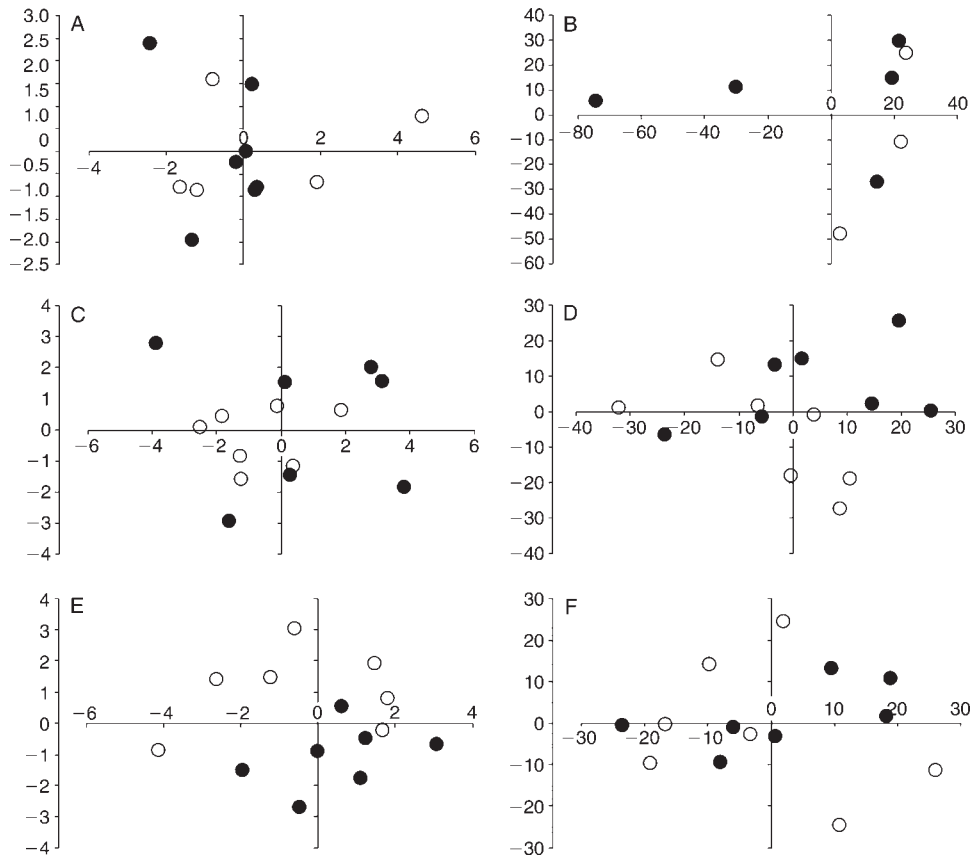


FIG. 4. PCOs of (A, C, E) vegetation structure and (B, D, F) bird communities for (A, B) 1–2 yr old, (C, D) 6–7 yr old, and (E, F) 11–13 yr old restoration. Desirable states (solid circles) and deviated states, either sparse or overdense (open circles), were not significantly different from one another for any restoration age for either vegetation structure or bird communities.

different from all other states ($t_{10} \geq 2.88$, $P \leq 0.003$), as were avian communities in unmined forest ($t_{12} \geq 2.08$, $P \leq 0.004$). However, avian communities in 6–7 yr old restoration were not significantly different from either 11–13 yr old ($t_{12} = 1.17$, $P = 0.217$) or 16–18 yr old postburn restoration ($t_{12} = 1.34$, $P = 0.059$), and avian communities did not differ significantly between 11–13 yr old and postburn restoration ($t_{12} = 1.40$, $P = 0.086$).

Overall bird abundance differed significantly among desirable states ($F_{4,30} = 35.97$, $P < 0.001$). Overall abundance in 1–2 yr old restoration was significantly less than all other treatments, while 16–18 yr old postburn restoration and unmined forest did not differ in overall bird abundance, but both had significantly fewer birds than both 6–7 yr old and 11–13 yr old restoration, although the latter two did not differ significantly from one another (Fig. 5). Site species richness also differed significantly among desirable states ($F_{4,30} = 85.76$, $P < 0.001$). Species richness in 1–2 yr old restoration was significantly less than other treatments and unmined forest sites had more species than 11–13 yr old and 16–18 yr old postburn restoration, but differences from 6–7 yr old restoration were marginally nonsignificant (Fig.

5). Species richness did not differ significantly among 6–7 yr old, 11–13 yr old, and postburn restoration (Fig. 5).

At the species level, 17 of 23 species showed significant differences in relative abundance among desirable states (see Appendices B and C). All common species differed in density among desirable states (see Appendix B). Striated Pardalotes were more abundant in unmined forest than in any age of restoration, but the remaining species were all most abundant in either 6–7 yr old or 11–13 yr old restoration (Fig. 6), although whether they were significantly more abundant than in other states differed among species. For frequent and uncommon species, the most common pattern was for species to be more abundant in unmined forest than any of the restored states (Red-capped Parrot, Spotted Pardalote, Western Thornbill, Western Yellow Robin, and Scarlet Robin; see Fig. 7). However, White-naped Honeyeaters increased in abundance as restoration matured and were most abundant in unmined forest, White-breasted Robins were most abundant in 6–7 yr old restoration, and Australian Pipits were more abundant in 1–2 yr old restoration than other desirable states (Fig. 7).

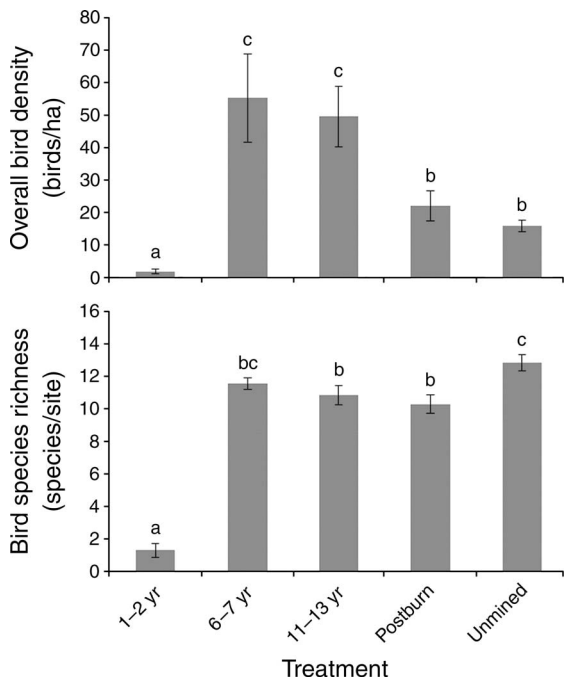


FIG. 5. Overall bird density and bird species richness (mean \pm SE) among the five desirable states. Letters above the standard error bars denote means that are significantly different ($P < 0.05$).

Do avian communities in deviated states differ from desirable states of the same age?

There were no significant differences in the bird community between desirable and deviated states for any age of restoration. The difference between desirable and sparse 1-2 yr old restoration was nonsignificant (pseudo- $F_{1,6} = 1.07$, $P = 0.400$), as was the difference between desirable and overdense 6-7 yr old (pseudo- $F_{1,12} = 1.33$, $P = 0.210$) and 11-13 yr old restoration (pseudo- $F_{1,12} = 1.30$, $P = 0.250$). Overall numbers of birds did not differ between desirable and sparse 1-2 yr old restoration ($t_{10} = 0.12$, $P = 0.909$) nor between desirable and overdense 6-7 yr old ($t_{10} = 1.72$, $P = 0.112$) and 11-13 yr old restoration ($t_{10} = 0.21$, $P = 0.836$). Bird species richness also did not differ between desirable and sparse 1-2 yr old restoration ($t_{10} = -0.14$, $P = 0.889$), nor between desirable and overdense 6-7 yr old ($t_{10} = 1.24$, $P = 0.239$) and 11-13 yr old restoration ($t_{10} = 0.00$, $P = 1.000$).

At the species level, none of the three common, frequent, or uncommon species recorded in 1-2 yr old restoration differed in relative abundance between desirable and sparse states (see Appendix D). Of the 15 common, frequent, or uncommon species recorded in 6-7 yr old restoration, only Western Gerygones differed significantly in relative abundance between the states ($t_{10} = 3.61$, $P = 0.004$), being significantly more abundant in

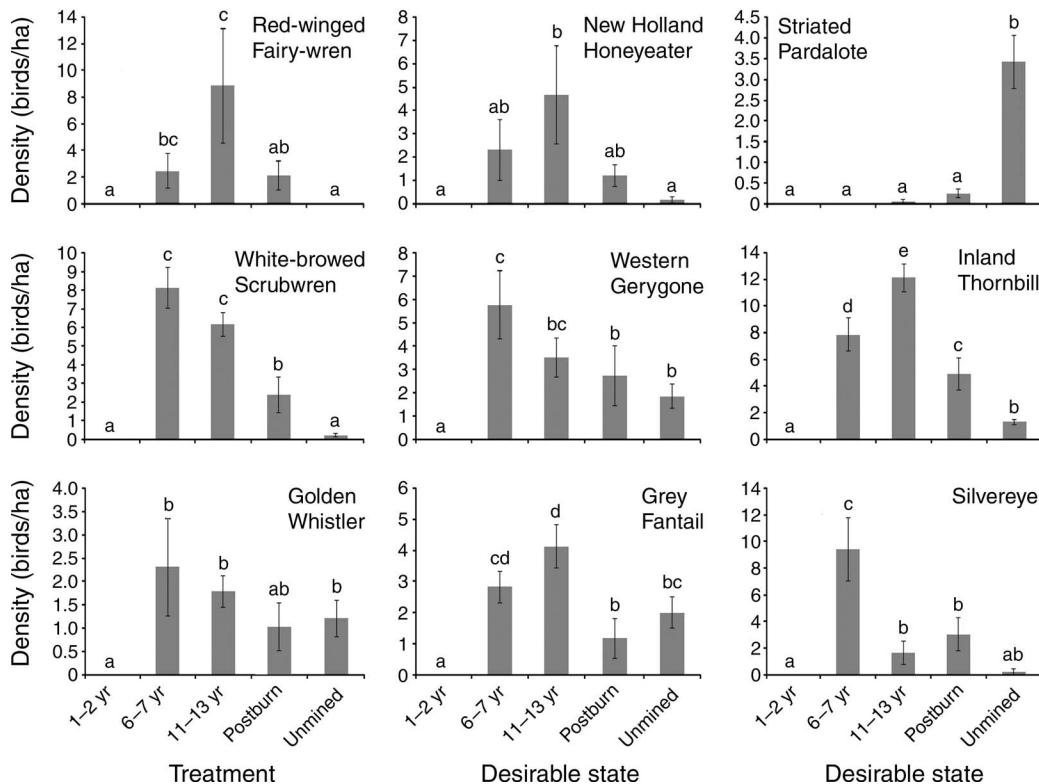


FIG. 6. Densities (mean \pm SE) of the nine common bird species, all of which showed significant treatment differences. Letters above the error bars denote means that are significantly different ($P < 0.05$).

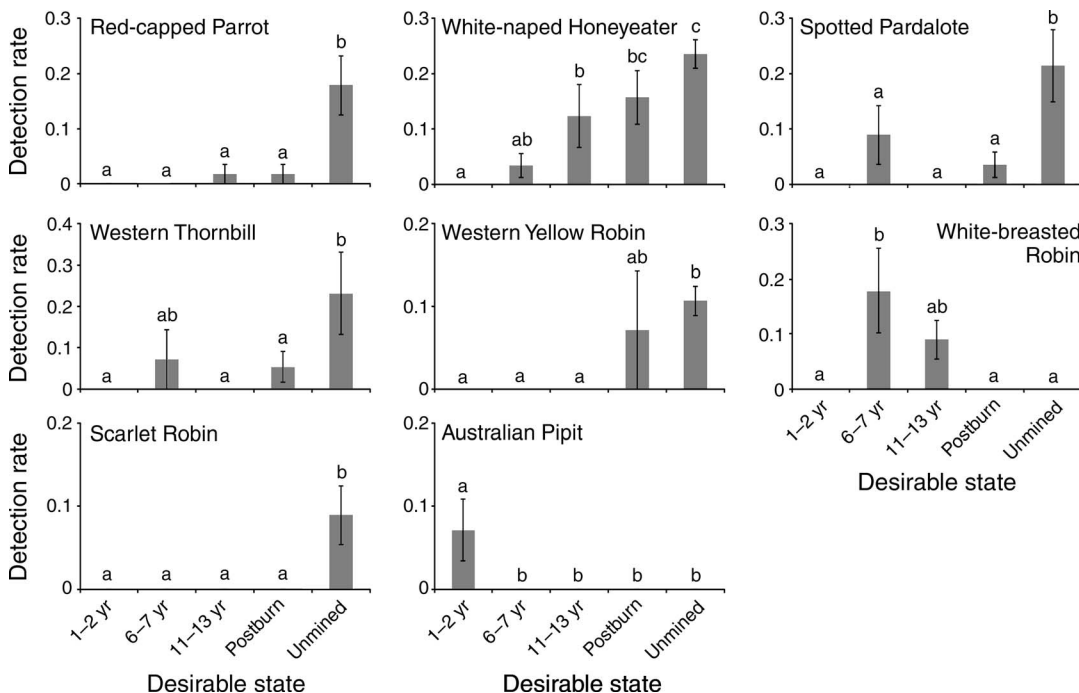


FIG. 7. Detection rates (proportion of point counts detected; mean \pm SE) of the eight frequent and uncommon species that showed significant treatment differences. Frequent species are the White-naped Honeyeater, Spotted Pardalote, Western Thornbill, and White-breasted Robin; uncommon species are the Red-capped Parrot, Western Yellow Robin, Scarlet Robin, and Australian Pipit. Letters above the error bars denote means that are significantly different ($P < 0.05$).

desirable than overdense restoration (0.52 ± 0.08 vs. 0.16 ± 0.05 birds/count, mean \pm SE; see Appendix D). Of the 14 common, frequent, or uncommon species recorded in 11–13 yr old restoration, none differed significantly in relative abundance between desirable and overdense states (Appendix D).

If there is no congruence between the state-and-transition models for vegetation and avian succession, why do they differ?

Relationships between vegetation structure and avian communities.—Structural variables explained much of the variation in avian communities among states (adjusted r_2 of best model = 0.39) and marginal tests from the DISTLM revealed that all structural variables were significantly related to the avian community (pseudo- $F_{1,31} > 2.54$, $P < 0.037$) except for legume density (pseudo- $F_{1,31} = 1.29$, $P = 0.211$) and eucalypt density (pseudo- $F_{1,31} = 1.34$, $P = 0.230$). For community metrics, no model had a $\omega_i > 0.1$, but summed variable weights revealed that cover from 1 to 2 m and overstorey density had the strongest relationship with overall bird abundance, while cover from 1 to 2 m and canopy height had the strongest relationship with bird species richness.

Relationships between vegetation structure and bird species.—For individual species, no models had a $\omega_i > 0.1$. Summed variable weights revealed that species showed a significant relationship most frequently with canopy height, litter cover, and CWD volume (Table 1).

These three variables, plus cover from 0 to 1 m and overstorey density, were the variables that had a summed model weight >0.5 for the most species. Conversely, eucalypt density and cover from 0 to 1 m were each significantly related to just one species (Golden Whistler and Weebill, respectively), while cover from 2 to 5 m and eucalypt density, again, had summed model weights >0.5 for only two species (Table 1). Legume density was significantly related to the density of two species (Western Gerygone and Striated Pardalote) and had summed model weights >0.5 for only four species (Table 1).

DISCUSSION

Given that one critical aspect of Grant’s state-and-transition successional model (STM) was to identify deviated states that required management to drive them onto a desirable pathway, we concluded that Grant’s STM based on vegetation succession did not accurately represent avian succession. Although our study found that avian communities generally showed significant differences among different desirable states, it found essentially no differences between avian communities in desirable and deviated states of the same restoration age. This difference in congruence between desirable and deviated states suggests that management practices designed to maintain vegetation succession on a desirable pathway may not have the same effect on avian communities (Stringham et al.

TABLE 1. The relationships between avian variables and the structural and floristic variables explored using multimodel inference for the study at Alcoa of Australia's Huntly Mine in Western Australia.

Bird variable	<i>n</i>	LiC	0-1	1-2	2-5	Leg	Euc	UnD	OvD	CHt	CWD
Community metric											
Overall bird abundance	1648	0.95**	0.99***
Bird species richness	38	...	0.60	0.81*	0.69	1.00***	...
			+	+	+					+	
Species											
Red-capped Parrot	15	...	0.66	0.98**	0.99***
Australian Ringneck	6	0.92*	0.72	0.99***	...
Red-winged Fairy-wren	117	1.00***
Splendid Fairy-wren	37	0.86*
Western Spinebill	48	0.71*	...
New Holland Honeyeater	96	0.50	0.89*
White-naped Honeyeater	59	0.55	1.00***	...
Western Wattlebird	9	0.70	...	1.00***	0.51	1.00***
Spotted Pardalote	20	0.56	0.98**	0.51
Striated Pardalote	79	0.87*	0.79*	1.00***	...
White-browed Scrubwren	178	0.82*	...	0.55	0.70*	0.84*	...
Weebill	18	...	0.94*	0.68	0.72	...
Western Gerygone	141	0.99**	0.99***	...	0.91*	...	0.86*	...
Inland Thornbill	277	0.65	0.64	0.57	0.63	0.78*
Western Thornbill	33	0.82*	0.61	1.00***	0.96**
Dusky Woodswallow	8
Golden Whistler	104	0.89*	0.72*	0.52	...
Gray Fantail	154	0.94**	0.58	0.59
Western Yellow Robin	11	0.78*	0.66	0.99**	...
White-breasted Robin	36	0.78*	0.94**	0.74*	...	0.61	...
Scarlet Robin	7	...	0.69	0.69	1.00***	...
Tree Martin	60	0.59
Silvereye	98	1.00***
Australian Pipit	7	...	0.53
No. spp. with summed variable $\omega_j > 0.5$	9		6	5	2	4	3	4	6	17	6
No. spp. related significantly to variable	8		1	2	2	2	1	3	3	11	4

Notes: Values shown are the summed models weight for all models from the entire model set that contained that particular structural or floristic variable. Also shown is the direction of the relationship (+ or -) and the probability that the model-averaged parameter value is significantly different from 0. Variables abbreviations are as follows: LiC, Litter cover; 0-1, cover from 0 to 1 m; 1-2, cover from 1 to 2 m; 2-5, cover from 2 to 5 m; Leg, legume density; Euc, eucalypt density; UnD, understory density; OvD, overstory density; CHt, canopy height; CWD, coarse woody debris volume; *n*, number of individuals detected of each species. Ellipses indicate no strong relationship (summed model weights were <0.4) between the bird variable (rows) and the vegetation variable (columns).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

2003), yet, given the critical role that fauna play in many ecosystem processes, it is crucial that the model also reflects faunal succession if it is to help achieve restoration outcomes that benefit all biodiversity. Furthermore, understanding why this difference in congruence occurs between desirable and deviated states can provide novel insights into how to develop state-and-transition models that better represent faunal succession.

Do various successional states on a desirable trajectory represent different avian communities and can further additional successional states be identified?

Grant's STM based on vegetation succession represented succession in avian communities in desirable states reasonably accurately. Avian communities in both unmined forest and 1–2 yr old restoration differed significantly from all other states, and many species were significantly more, or less, abundant in these two states than in other states, as is typical of postmining restoration. Furthermore, we found no difference in the avian community between 6–7 yr old and 11–13 yr old restoration justifying the grouping of both ages into a single state of 5–15 yr old restoration in Grant's STM. The only lack of congruence with the state-and-transition model based on vegetation succession was that avian communities in 16–18 yr old postburn restoration were not significantly different, although only marginally so, from communities in 6–7 yr old and 11–13 yr old restoration. However, the reduction in abundance of many shrub-dependent species (e.g., White-browed Scrubwren, Inland Thornbill, and Gray Fantail) in postburn restoration suggests that its avian communities are likely different from those in 6–13 yr old restoration and that the addition of more sites may have resulted in significant differences being observed.

Despite the model successfully representing avian community succession, there was some divergence between the differences in vegetation structure and avian communities among states. Unmined forest and 1–2 yr old restoration were the most different from other states in both their vegetation structure and the avian community composition, as is typical in restored forests (e.g., van Aarde et al. 1996, Gardali et al. 2006, Brady and Noske 2010), but avian communities did not differ significantly between 6–7 yr old and 11–13 yr old restoration, although vegetation structure did. Furthermore, avian communities in 16–18 yr old postburn restoration were more similar to those in 11–13 yr old restoration than 6–7 yr old restoration, although differences in vegetation structure showed the opposite pattern. Given the fundamental importance of forest structure in influencing forest bird community composition (e.g., Jayapal et al. 2009, Uezu and Metzger 2011), this lack of congruence is surprising. The patterns we observed suggest a nonlinear relationship, however, whereby when vege-

tation structure is very different, avian communities are also likely to be, but the congruence with differences in avian communities starts to weaken as vegetation structure becomes more similar. This nonlinear relationship supports the idea that state-and-transition models best represent differences in ecological communities when they represent different plant communities with fundamentally different vegetation structures that are separated by an ecological threshold, rather than different seral stages of the same plant community that are more similar in terms of vegetation structure (Holmes and Miller 2010, Knapp et al. 2011).

Do avian communities in deviated states differ from desirable states of the same age?

In contrast to states along a desirable trajectory, the state-and-transition model did not accurately represent differences in the avian community between desirable and deviated states of the same age. None of the avian communities in the deviated states differed significantly from the desirable states of the same age, and only a single species, the Western Gerygone, differed in abundance between a deviated and desirable state of the same age. As for desirable states, there was also some divergence between similarities in vegetation structure and avian communities. Deviated 11–13 yr old restoration had taller canopies and more canopy cover (the latter highly correlated with litter cover) than desirable 11–13 yr old restoration, however, although these variables appeared important in structuring avian communities, the avian community did not differ significantly between these states. The main reason why the state-and-transition model did not accurately represent avian succession was the fact that deviated and desirable states of the same restoration age neither differed significantly in overall vegetation structure nor in the variables on which their classification was based. Although sparse 1–2 yr old restoration had lower legume (and understory) densities than desirable 1–2 yr old restoration and overdense 6–7 yr old and 11–13 yr old restoration had higher eucalypt (and overstory) densities than desirable 6–7 yr old and 11–13 yr old restoration, none of these differences were significant. As the deviated states in the state-and-transition model were based on legume and eucalypt densities at 9 months postmonitoring, our results suggest that restored areas may need to be monitored repeatedly over extended time frames if they are to accurately represent deviations in both vegetation and avian succession.

If there is no congruence between the state-and-transition models for vegetation and avian succession, why do they differ?

Our study indicated that Grant's STM based on vegetation succession did not accurately represent avian succession and that there was a lack of

congruence between vegetation and avian succession. Understanding factors that likely caused this lack of congruence can help identify ways to develop state-and-transition models that better represent both vegetation and faunal succession. The first factor that may explain why Grant's STM did not accurately represent avian succession was the fact that it did not successfully represent succession in vegetation structure either. Overall vegetation structure did not differ significantly between deviated and desirable states of the same age, and very few vegetation variables differed between the states. This implies that, structurally, deviated and desirable states were not significantly different and, consequently, we would not have expected avian communities to differ significantly between states of the same restoration age either. Furthermore, at the time of our study, deviated states no longer differed significantly from the desirable states of the same age in the criteria by which the states were defined. Sparse states had lower legume densities and overdense states had higher eucalypt densities than desirable states, but the differences were not significant. This implies that sites need to be continually monitored, rather than simply monitored nine months post-disturbance, and any changes in the classification of sites continually updated if state-and transition models are to successfully represent successional processes (Briske et al. 2005). This is particularly important if the disturbance is severe, as with mining, as we would expect sites to change considerably post-disturbance. It is widely acknowledged that state-and-transition models should be considered as working hypotheses that need to be continually evaluated and refined if they are to ensure the application of sound management prescriptions (Briske et al. 2005, Knapp et al. 2011).

Another factor that may have contributed to the lack of congruence between vegetation and avian succession was that desirable and deviated states were separated by ecologically arbitrary values (2500 eucalypt stems/ha and 0.5 legumes/ha) that were merely points along a continuum, rather than ecological thresholds that represented points where the vegetation community transitioned rapidly to a different vegetation community. While state-and-transition models can be used to represent continuous, gradual transitions (Briske et al. 2005), they tend to more accurately represent ecological communities, and hence, presumably faunal succession as well, when states are separated by ecological thresholds that result from changes in ecological processes rather than community composition (Cortina et al. 2006). For instance, good congruence was found between faunal communities and state-and-transition models when states in the model represented different plant communities that were separated by ecological thresholds (Holmes and Miller 2010). It has been suggested that vegetation communities that replace one another along

traditional successional pathways should be grouped within a single state (Bestelmeyer et al. 2004), although, in reality, the delineation of states within state-and-transition models has been highly variable with both narrow and broad delineations (Stringham et al. 2003). Managing restored areas typically involves managing succession in a single vegetation community, which then poses a challenge for developing state-and-transition models that accurately represent successional processes within restored areas and, hence, accurately inform management. Our study suggests that developing models where states are separated by thresholds and defined by ecological processes are most likely to accurately represent faunal succession but, in the absence of knowledge to build such models, at least defining states based on ecologically meaningful values should improve the ability of such models to accurately inform management.

A further factor that likely contributed to the lack of congruence between vegetation and avian succession in Grant's STM was that states were defined by vegetation features that were not important in structuring the avian community. Eucalypt density was the vegetation variable that showed the fewest relationships with the avian community and legume density also showed relatively few relationships. A state-and-transition model that showed good congruence with Grasshopper Sparrow (*Ammodramus saviarum*) abundance contained states that were defined by their cover of perennial bunchgrass (Holmes and Miller 2010), which is known to be an important variable affecting Grasshopper Sparrow abundance (Vander Haegen et al. 2000, Earnst et al. 2009). Other studies that have modeled predicted population changes of Sage Grouse using state-and-transition models have delineated states within the model based on understory composition and structure and dominant canopy vegetation (Hemstrom et al. 2002, Wisdom et al. 2002), which, again, are known to be variables important in influencing Sage Grouse abundance (Swanson et al. 2013, Whitehurst and Marlow 2013). These studies suggest that state-and-transition models based on vegetation variables can accurately represent faunal communities, but only when the vegetation variables that delineate states are known to be ecologically important in influencing species abundances or community composition. Our analyses suggest that canopy height, litter or canopy cover, CWD volume, and overstory density are the vegetation variables that showed the most relationships with the avian community, and delineating states based on these variables may result in a state-and-transition model that better represents avian succession. However, it is also possible that vegetation variables that we did not measure, such as the density of large trees or nectar-producing plants (e.g., Kalies and Rosenstock 2013, Luck et al. 2013, Reidy et al. 2014), may be more important in structuring the bird

community, and future research should investigate this possibility.

The last factor that may explain the lack of congruence between vegetation and avian succession is that the value of variables that delineated states were not based on values in the reference community and, hence, all states may have effectively been in a deviated state. As restoration success often involves attaining the range of conditions found in the reference community (e.g., Grimbacher et al. 2007, So and Chu 2010, Gould 2012), management is often based around evaluating whether sites fall outside that range and then implementing management prescriptions to drive these deviated sites onto a desirable pathway (De Steven et al. 2010). While the aim of Grant's STM was to identify deviated states, the criteria used to define states were not related to values in reference sites. Thus, of the vegetation variables that appeared most related to the avian community, all restored sites had less CWD and shorter canopies than all unmined sites, and only seven of the 47 restored sites (<15%) had litter and canopy cover values within one standard error of the mean values for those variables in unmined forest. Furthermore, unmined sites showed no overlap with any restored sites in terms of overall vegetation structure (see Fig. 2), suggesting that most, or all, restored sites may have been in a deviated state. While the question of how quickly states can resemble the reference state remains, our results suggest that defining restoration states based on criteria that relate to the range of conditions found in the reference state may more effectively identify desirable states, deviated states that require management to drive them onto a desirable pathway, and accelerate restoration succession toward the reference community.

There are other factors that may have also contributed to the lack of congruence between vegetation and avian succession. The first is the importance of non-vegetation factors, such as resource availability, in structuring faunal communities (e.g., Letnic and Dickman 2010, Edworthy et al. 2011, Lawrence et al. 2013), which means that vegetation structure may be poorly correlated with faunal communities in some ecosystems. Alternatively, the lack of congruence between vegetation and avian succession may result from a mismatch between the spatial scale over which structural variables were measured and the spatial scale over which birds move (Morzillo et al. 2012). Therefore, any state-and-transition model based on vegetation succession in our study system is more likely to accurately represent avian succession for species whose home range size is the same, or smaller, than the average pit size (~20 ha; Nichols and Nichols 2003). A model that aims to represent bird species with home range sizes larger than 20 ha may need to include landscape variables (e.g., proportion of unmined forest within a certain radius) as criteria to classify pits into each restoration state (Briske et al. 2005), although a previous study in similarly unfrag-

mented mining landscapes did not find any significant landscape influences on the bird community in restored areas (Gould 2011).

MANAGEMENT IMPLICATIONS

Our study found that using Grant's STM to manage successional pathways in restored bauxite mine pits in the jarrah forest of southwestern Australia would not have effectively managed avian succession in those mine pits. While the influence of mismanaging avian succession on vegetation succession and ecological processes in the mine pits is unknown, given the importance of birds in various ecosystem processes (e.g., pollination; Sargent and Ackerly 2008, Phillips et al. 2010), effectively managing all biodiversity in mine pits would maximize the chances of restoration success (Forup et al. 2008). While overstory thinning, the main management strategy proposed by Grant's STM to drive deviated states onto a desirable pathway (Grant 2006), is unlikely to have long-term negative impacts upon the avian community, obtaining data to determine that remains desirable. State-and-transition models are limited to the scope of information used to construct them (Morzillo et al. 2012), and so the continuing revisions of Grant's STM will increasingly represent both vegetation and avian succession only if more information continues to become available.

CONCLUSION

Given the utility of STMs in conceptualizing successional processes, it is likely that they will continue to be used extensively as a tool to inform management of post-disturbance succession (Knapp et al. 2011, Rumpff et al. 2011). Fauna are less frequently considered in STMs than vegetation yet, given the importance of fauna in many ecosystem processes (e.g., Thornton et al. 1996, Phillips et al. 2010), it is likely that for STMs to effectively inform management they will need to accurately reflect faunal, as well as vegetation, succession. Our study suggests that assuming that faunal succession will follow patterns of vegetation succession (Suding 2011) is unlikely to hold in many ecosystems, and we identified four factors that should be considered in the development of STMs to improve their ability to represent faunal, as well as vegetation, succession. These are to (1) conduct long-term monitoring of succession in all states and use this information to update and improve models; (2) define states based on criteria that are important in structuring the faunal community; (3) where possible, define states based on ecological processes and thresholds; and (4) in restoration, define states based on criteria that relate to values in the reference community. We believe that considering these factors when developing STMs should improve their ability to accurately represent faunal succession. Developing state-and-transition models that better incorporate patterns of faunal

succession should improve the ability to manage post-disturbance succession across a range of ecosystems for biodiversity conservation.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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