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RESEARCH ARTICLE

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Livestock grazing reinforces the competitive exclusion of small-bodied birds by large aggressive birds

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Abstract

1. Grazing by domestic livestock is sometimes promoted as a management tool to benefit biodiversity. In many situations, however, it can produce negative outcomes.
2. Here, we examine the impacts of recent and historic livestock grazing on bird communities in the semi-arid woodlands in eastern Australia, testing the notion that grazing removes the suppressive effect of structurally complex vegetation on miners, thereby reducing the richness and abundance of small birds.
3. We used time- and area-limited searches of 108 sites varying in livestock grazing history and intensity, to explore the direct and indirect effects of grazing, habitat complexity and the abundance of aggressive, large-bodied birds on smaller-bodied birds using two-way analysis of variance and structural equation modelling.
4. Small birds were less abundant and had lower richness in the presence of miners. Our structural equation models indicated that recent grazing had direct suppressive effects on the abundance of miners, and both richness and abundance of all but the largest-bodied bird groups. However, higher levels of historic livestock grazing reinforced the competitive exclusion of the six small-bodied bird groups (insectivores, nectarivores, declining woodland birds, small ground-foraging birds, all small birds and all non-miners) by aggressive miners via reductions in habitat complexity. Moreover, the strength of any suppressive effects on small birds or positive effects on large birds by miners increased with increasing miner abundance.
5. *Synthesis and applications*. Our results highlight the importance of vegetation structural complexity, not only for providing habitat for woodland birds, but also as barriers to the invasion and competitive dominance of miners. Our findings suggest that management actions aimed at reducing tree and shrub density to promote open woodlands are likely to have significant negative consequences for the conservation of small woodland birds.

KEYWORDS

competition, habitat complexity, livestock, *Manorina* miners, small-bodied birds, tree density, woodland birds

1 | INTRODUCTION

Birds have suffered marked range reductions over the past century with dramatic declines reported for central and northern America, Europe, Africa, Asia and Australasia (Brennan & Kuvlesky, 2005; Sanderson, Donald, Pain, Burfield, & van Bommel, 2006; Thomas et al., 2004). Declines in bird populations are typically associated with the direct effects of human-induced habitat loss and landscape degradation, competition for resources, and sometimes, overhunting and predation (Pimm & Askin, 1995). There is increasing evidence, however, that the indirect effects of human-altered landscapes may outweigh the effects of habitat loss (Byers, 2002).

Indirect effects are most commonly seen where an increase in abundance and distribution of one species negatively affects another species via competitive effects or increased predation or parasitism. This can lead to cascading changes in resource availability, nutrient cycles and ecosystem processes, often resulting in a loss of ecosystem functions through reduced functional trait diversity (Mayfield et al., 2010) and intensified interspecific competition. In more severe cases, shifts in interspecific competition results in competitive displacement (Reitz & Trumble, 2002), where formerly established species are completely lost from a locality. For example, increasing abundance of the house finch (*Carpodacus mexicanus*) has been shown to negatively affect the purple finch (*Carpodacus purpureus*) through competitive interactions following its reintroduction in New York (Wootton, 1987). In North America, long-distance migrants are threatened by the increase in abundance of birds favouring suburban habitats (Askins & Philbrick, 1987). Non-indigenous species with aggressive traits may have a greater competitive ability in altered environments (Byers, 2002) leading to the extirpation of local species. Finally, landscape alterations can increase the distribution of competitors, resulting in intensified competition in some habitats, such as occurs with the bell miner (*Manorina melanophrys*) in eastern Australia (Kavanagh & Stanton, 2003).

In woodlands and forests in eastern Australia, increases in the abundance of large-bodied aggressive birds, such as the noisy miner (*Manorina melanocephala*) and bell miner, are associated with marked declines in populations of small-bodied birds (Ford, Barrett, Saunders, & Recher, 2001; MacNally, Bowen, Howes, McAlpine, & Maron, 2012; Maron et al., 2013) and substantial shifts in composition and community assemblage (Piper & Catterall, 2003). The declining status of many small woodland birds is of national concern (Ford et al., 2001) and interspecific competition by aggressive miners is regarded as one of the most significant and widespread processes threatening woodland birds (Maron et al., 2011). Studies have shown that many factors influence the level of interspecific competition, including landscape fragmentation and habitat degradation (Robertson, McAlpine, House, & Maron, 2013), thinning and logging (Eyre, Ferguson, Kennedy, Rowland, & Maron, 2015), structural simplification (Maron et al., 2013), higher mean rainfall and closer proximity to edges (Thompson et al., 2015), altered fire regimes and woodland community type (Maron & Kennedy, 2007), and potentially even climate change (Bennett, Clarke, Thomson, & MacNally, 2014). Less well known, however, is the influence that livestock grazing has on the mechanisms that regulate levels of interspecific competition between miners and small birds.

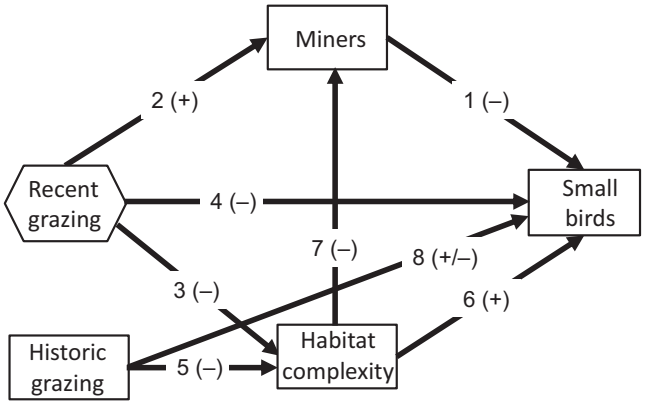

FIGURE 1 A priori model depicting the effects of recent livestock grazing (using dung counts), historic livestock grazing (using livestock track density/size), habitat complexity (sensu Watson et al., 2001), miner abundance and different guilds of birds. Numbers correspond to pathways (and their hypothesised direction) identified in Table 1

We had three hypotheses relating to the interactions between livestock grazing, habitat structure, miners and bird groups. First, we expected that the presence of miners would reduce small bird richness and abundance, consistent with results from fragmented woodlands in eastern Australia, but largely untested in intact woodlands (Figure 1, Pathway 1, Table 1). Second, we expected small bird abundance and/or richness to be reduced indirectly by domestic grazing effects on habitat complexity (Pathway 6 via 3 or 5). Small woodland birds prefer large, structurally complex and well-connected habitat patches (Watson, Freudenberger, & Paull, 2001; Pathway 6). Grazing by European livestock, however, can alter this structure by removing mid-storey vegetation and preventing its regeneration (Dorrough et al., 2012; Tiver & Andrew, 1997), thereby increasing the risk of predation. Grazing can also modify grass and litter layers, thereby reducing invertebrates for ground-foraging birds (e.g. Bromham, Cardillo, Bennett, & Elgar, 1999; Pathways 3 and 5). Thus, grazing could reduce small bird abundance and/or richness indirectly by reducing habitat complexity (Pathway 6 via 3 or 5 via 3). Our third hypothesis relates to the untested mechanisms linking grazing effects with reduced habitat complexity leading to greater miner abundance and flow on effects on small birds. Increased grazing could alter vegetation complexity and therefore predispose sites to invasion by miners (Pathway 7 via 3 or 5), which are advantaged by habitat fragmentation and structural simplification (Maron et al., 2013). Consequently, changes in vegetation structure could conceivably affect both miners (Pathway 7) and small-bodied birds (Pathway 6), but in opposite directions. We tested these hypotheses using data on recent and historic grazing by domestic livestock from a large regional grazing study across three woodland communities in semi-arid eastern Australia.

2 | MATERIALS AND METHODS

2.1 | The study area

We surveyed a total of 108 sites, 36 replicate sites in each of three broad vegetation communities dominated by either *Callitris*

TABLE 1 Hypothesised mechanisms underlying the grazing-miner-habitat complexity a priori model in Figure 1

Path	Hypothesised mechanisms
1	(−) Miners are a highly aggressive communal species that competitively exclude small birds, predominantly small insectivores, reducing their occurrence rates and abundance (MacNally et al., 2012)
2	(+) Heavily grazed areas are thought to be preferred by miners (Eyre et al., 2009; Howes & Maron, 2009; Martin, Kuhnert, Mengersen, & Possingham, 2005)
3	(−) Grazing modifies the grass and litter layers, the habitat for invertebrates (Bromham et al., 1999), suppresses shrub recruitment and regeneration (Tiver & Andrew, 1997), and increases bare ground and reduced grass height (Van Doorn, Woinarski, & Werner, 2015)
4	(−) Grazing by domestic stock is regarded as a threatening process for birds in the arid zone (Reid, 1999), bird abundance and richness declines under livestock grazing (Dorrough et al., 2012)
5	(−) Grazing by livestock leads to a loss of understorey vegetation, restricts regeneration of the shrubs and trees, and leads to an alteration of the grass and herb layer (Ford et al., 2001)
6	(−) Small insectivores and woodland birds generally increase with increasing habitat complexity (Cousin & Philips, 2008; Watson et al., 2003)
7	(−) Noisy miners are advantaged by structural simplification (Maron et al., 2013) and proliferate in areas of open, lightly-treed areas (Ashley et al., 2009) and sites with little or no shrub cover (Higgins, Peter, & Steele, 2001; Howes & Maron, 2009; Major et al., 2001)
8	(+/−) Prolonged high levels of livestock grazing shifts bird assemblages from small-bodied birds to large-bodied generalists (Martin & Possingham, 2005). Small understorey foraging bird species generally decline with increasing grazing pressure (Martin & McIntyre, 2007). Grazing negatively affects both resident and migratory birds dependent on ground cover and seeds for over winter survival (Bock & Bock, 1998)

glaucophylla (Joy Thomps. and L.A.S. Johnson), *Eucalyptus largiflorens* (F. Muell) or *Eucalyptus camaldulensis* (Dehnh). The study area spanned 0.3 million km^2 of eastern Australia in the central-west and parts of western New South Wales. Mean annual rainfall ranges from 385 to 460 mm, and average temperature is *c.* 18°C, but varied little across the area. Soils are dominated by clay loams and loams. Sites were selected from a total pool of 451 where vegetation, soils and grazing intensity data had previously been collected (Eldridge, Delgado-Baquerizo, Travers, Val, & Oliver, 2017). Sites were selected to span the available range of grazing intensities (see below) and habitat conditions (i.e. groundstorey plant, woody plant and litter cover).

2.2 | Assessment of habitat and grazing intensity data

At each site, we positioned a 200 m long transect, which formed the central axis of the 2 ha bird survey plot (200 m × 100 m). Along the transect, we assessed the projected crown cover of trees (>4 m tall), shrubs (0.5–4 m), grasses and other groundstorey plants (<0.5 m) every 2 m. We placed five 25 m^2 (5 m × 5 m) plots (hereafter "large quadrat") every 50 m (i.e. 0, 50, 100, 150 and 200 m) along the transect. Within each large quadrat, we centrally nested a smaller (0.5 m × 0.5 m) quadrat (hereafter "small quadrat"). In each quadrat, we assessed the cover of litter, coarse woody debris, biological soil crusts and bare soil. To assess the density of shrubs and saplings, we used a variable width 200 m belt transect, counting into two separate size classes "tall" (1.3–3 m) and "short" (0.5–1.3 m). All quadrat level data were averaged at the site level.

Grazing was assessed using measures of recent and historic grazing pressure. To assess the level of historic grazing, we measured the width and depth of all livestock tracks crossing the 200 m transect and calculated the total cross-sectional area (cm^2) for each 200 m transect. Track density has been used previously as a surrogate for the long-term use of sites by livestock (e.g. Lange, 1969; Pringle & Landsberg, 2004). The use of track density as a grazing surrogate is reflects the fact that a greater density and depth of tracks reflects longer periods of use by livestock (Pringle & Landsberg, 2004), particularly historic use. We acknowledge, however, that grazing is a highly complex issue, and the pattern of grazing is influenced by many factors, including, but not limited to, the distribution of vegetation, the location of water points and the nature of the surrounding landscape. Tracks may be more well-developed where there is only one water point or on soils that have a have higher clay content. In our study, all sites were served by only one water point, thereby ruling out any confounding effects of overlapping tracks from different watering points. We believe, therefore, that our measure of track density was a reasonable surrogate of an integrated level of historic livestock grazing.

To assess recent grazing, we counted dung pellets of different herbivores in both the small and large quadrats, separately, for each type of herbivore. Dung and pellet counts are used widely to estimate large herbivore abundance (Johnson & Jarman, 1987; Marques et al., 2001). Kangaroo (*Macropus* spp.), rabbit (i.e. rabbits and hares; *Oryctolagus cuniculus* L. and *Lepus europaeus* Pallas) and sheep (which included sheep *Ovis aries* L. and goats *Capra hircus* L.) dung pellets were counted in the small quadrats, and cattle dung (*Bos taurus* L.), sheep and kangaroo dung pellets were counted in the large quadrats. For cattle, we counted dung events rather than individual fragments, i.e. we considered a number of small fragments to have originated from one dung event, if the fragments were within an area of a few metres. At 10 sites, we counted, collected, dried and weighed the dung from 10 large quadrats to obtain a relationship between dung counts and dry mass for each herbivore. This relationship was then used to calculate the total oven-dried mass of dung per hectare per herbivore

as our measure of recent grazing intensity. Where dung from the same herbivore was assessed in both the large and small quadrats, we derived an average mass per hectare based on both quadrats for that herbivore type.

2.3 | Bird surveys and groups

At each site, we recorded the abundance of all birds, by species, using a standard 20-min 2 ha search (Barrett, Silcocks, Barry, Cunningham, & Poulter, 2003). All sites were sampled in the morning, twice in Spring 2014 and twice in Spring 2015. Prior to any analyses, bird records from the four visits over the 2 years were pooled to provide a measure of total richness (number of species) and abundance. All species were assigned to one or more of eight groups based on foraging strategy and body size (Maron et al., 2013): all birds (excluding *Manorina* spp.), all small-bodied birds (birds <63 g, the mean body mass of the noisy miner; Piper & Catterall, 2003), small-bodied insectivores, small-bodied nectarivores, small-bodied ground-foraging birds, large-bodied (>63 g) birds, large-bodied ground-foraging birds and "declining woodland birds" (Watson et al., 2001). Separately, we assembled data on the abundance of miners *Manorina* spp.) for each site.

2.4 | Calculation of habitat complexity

For each site, we derived a habitat complexity score, modified from the score of Watson et al. (2001), comprising six habitat attributes: tree cover, ground cover, litter cover, coarse woody debris cover, and density of tall (1.3–3 m) and short (<1.3 m tall) shrubs (Table S1). These vegetation attributes have been shown to be strong predictors of the occurrence and diversity of birds (Ford et al., 2001). These attributes were rated on a scale of 0–3, with increasing values corresponding to greater cover or density. The final site level score was obtained by summing the scores for the six attributes and dividing by 18, the maximum possible score. Sites with a larger score therefore had greater habitat complexity. This score has been shown to be a useful predictor of the richness and abundance of ground-dwelling small mammals (Catling & Burt, 1995), and with a slight modification, the richness of woodland birds (Watson, Watson, Paull, & Freudenberger, 2003).

2.5 | Statistical analyses

We used a two-way ANOVA to examine differences in richness and abundance of the eight bird groups in relation to the presence or absence of minors, community type (Blackbox, Cypress pine, Red gum) and their interaction.

Structural equation modelling (SEM) was then used to analyse the effects of grazing and the abundance of miners on the richness and abundance of the eight bird groups. SEM partitions direct and indirect effects of one variable upon another and estimates the strengths of these multiple effects. This allows us to test the plausibility of a causal model, based on a priori information, in explaining the direct and indirect relationships among variables of interest.

We developed an a priori model based on existing knowledge of the effects of recent grazing, historic grazing, habitat complexity and miner abundance on richness and abundance of other birds (Figure 1). Hypothesised pathways in our a priori model were compared with the variance–covariance matrix of our data in order to calculate an overall goodness-of-fit using the χ^2 statistic. The goodness-of-fit test estimates the likelihood of the observed data given the a priori model structure. Thus, high probability values indicate that models are highly plausible causal structures underlying the observed correlations. Before fitting empirical data to our a priori models, we examined the univariate correlations among all variables and standardised (*z*-transformed) the data. The stability of the resultant models was evaluated as described in Reisner, Grace, Pyke, and Doescher (2013). Analyses were performed using the AMOS 22 (IBM, Chicago, IL, USA) software. For each of our models, those with low χ^2, high goodness-of-fit index (GFI) and high normal fit index (NFI) were interpreted as showing the best fit to our data.

Exploratory analyses of all eight bird groups indicated no effects of either kangaroo grazing or rabbit grazing. Consequently, in the final SEMs, we depicted "grazing" as a composite variable that represented the combined effects of grazing by recent livestock (cattle dung, sheep/goat dung) and historic grazing by livestock (cattle and sheep/goat tracks). We ran separate SEMs for each of the eight bird groups.

3 | RESULTS

We recorded a total of 3,963 occurrences of 131 bird species across the three communities and four surveys at each site. Miners occurred at 51 of the 108 sites (total of 139 occurrences ranging from one to eight birds; median = three birds across all sites).

Richness and abundance of nectarivores, declining woodland birds, small ground foragers, insectivores, all small birds and the total bird community (sum of all birds excluding miners) were always significantly lower in the presence of miners (ANOVA: $F_{2, 102} > 3.6$, $p < .03$; Figure 2). Conversely, the richness and abundance of large ground foragers and the sum of all large birds (excluding miners) were greater in the presence of miners (ANOVA: $F_{2, 102} > 32.1$, $p < .001$; Figure 2).

Increases in the intensity of recent grazing were associated with direct, and therefore unexplained, reductions in richness and abundance of most small bird groups (Figures 3 and 4), and increases in large bird groups (Figure S1). However, recent grazing did not affect small birds via changes in habitat complexity, as predicted in our a priori model (Pathway 6 via 3).

Historic grazing had a negative effect on habitat complexity across all models, but we only detected a suppressive effect of historic grazing on the richness of nectarivores via reductions in complexity (Figure 3c), providing little support for our second hypothesis.

Recent grazing had a slight suppressive effect on the abundance of miners (path coefficient [PC] = −0.15; Figures 3 and 4). The sum of all direct and indirect effects (standardised total effects) indicated that miner abundance had the greatest suppressive effects on both

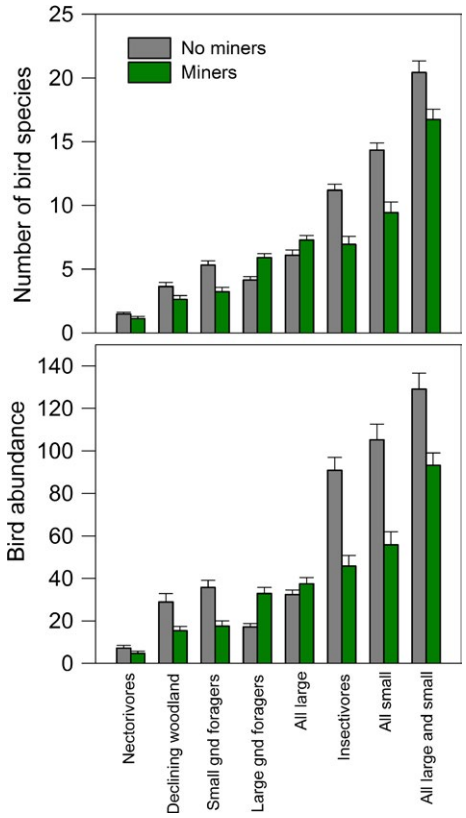

FIGURE 2 Mean (±*SE*) richness and abundance of all eight bird guilds in relation to presence or absence of miners [Colour figure can be viewed at wileyonlinelibrary.com]

richness and abundance of the five small bird groups, and the group containing all birds excluding miners (Table 2). This was followed by increases in historic grazing, at least for richness (Table 2). Increasing miner abundance increased the magnitude of any suppressive effects of miners on the richness or abundance of the small bird group (Figure 4a,b), specific small bird groups (Figure 3), or the positive effect on large birds (Figure S1). Interestingly, the total effect (STE) of increasing vegetation complexity on small birds was generally positive for richness, but for abundance only positive for small nectarivores (Table 2).

Our models also show that, for all but large ground foragers and all large birds other than miners, increasing levels of historic grazing reinforced the competitive exclusion of the six small bird groups (insectivores, nectarivores, declining woodland birds, small ground-foraging birds, all small birds and all non-miners) by aggressive miners, by reducing habitat complexity (Figures 3 and 4).

4 | DISCUSSION

Consistent with our hypotheses, the richness and abundance of small-bodied woodland birds, declined with increases in miner abundance, which was partly driven by grazing-induced reductions in habitat complexity. Although increases in the intensity of recent grazing had a slight direct suppressive effect on miner abundance, the direct suppressive effect on richness and abundance of other generally smaller birds was substantially greater. Overall, however, while the presence of miners had the greatest suppressive effect on small birds, increases in historic grazing also suppressed small birds, suggesting that legacy effects of historic grazing management practices have persisted ("the extinction debt" hypothesis sensu Tilman, May, Lehman, & Nowak, 1994).

4.1 | Miners suppress small birds and are associated with large birds

The most apparent result of our study was that miners reduced the richness and abundance of small birds (standardised total effect from −0.23 to −0.59), consistent with our first hypothesis. This result is consistent with research from highly fragmented woodlands in eastern Australia where miners monopolise entire patches for foraging (e.g. Thompson et al., 2015). In our study, however, this suppressive effect occurred in all communities, even relatively intact woodlands, and in communities dominated by *C. glaucophylla* where miner densities are generally low. Our study clearly showed that the small-bird assemblage was significantly different in the presence of miners, and that small insectivores and small ground-foraging birds were the foraging guilds most affected (Table 2).

Our study also revealed a positive association between the presence of miners and the two large bird groups. Of particular note was the higher abundance and richness of the large ground-foraging group, which was dominated by aggressive species, such as butcherbirds (*Cracticus* spp.), ravens (*Corvus* spp.), laughing kookaburras (*Dacelo novaeguineae*) and black-backed magpies (*Craticus tibicen*). Although the mechanisms linking higher miner numbers with higher numbers of other large birds were not elucidated by our study (see Figure S1), similar findings have been reported by others (Piper & Catterall, 2003; Thompson et al., 2015). Larger birds are thought to be tolerated by miners where they have a dissimilar diet or only a partial dietary overlay Piper and Catterall (2003) and it has been suggested that mutual benefits could arise from improved defence and food supplies (Maron et al., 2013). It is also possible that several of the large-bodied species are more common at sites with higher densities of miners because they prefer the more open and degraded sites that noisy miners frequently occupy. Our study shows that miners directly altered the bird assemblage structure, excluding small birds through their aggressive territorial behaviour, and were associated with greater richness and abundance of large birds, many of which are aggressive or specialised predators of small birds and their young or eggs (Piper & Catterall, 2003), therefore compounding the impact on small birds.

4.2 | Grazing-induced reductions in vegetation complexity suppress small-bodied birds

Our models show that a more complex vegetation structure was associated with greater richness of small birds, particularly nectarivores and insectivores (STE = 0.21–0.26). This is consistent with the second

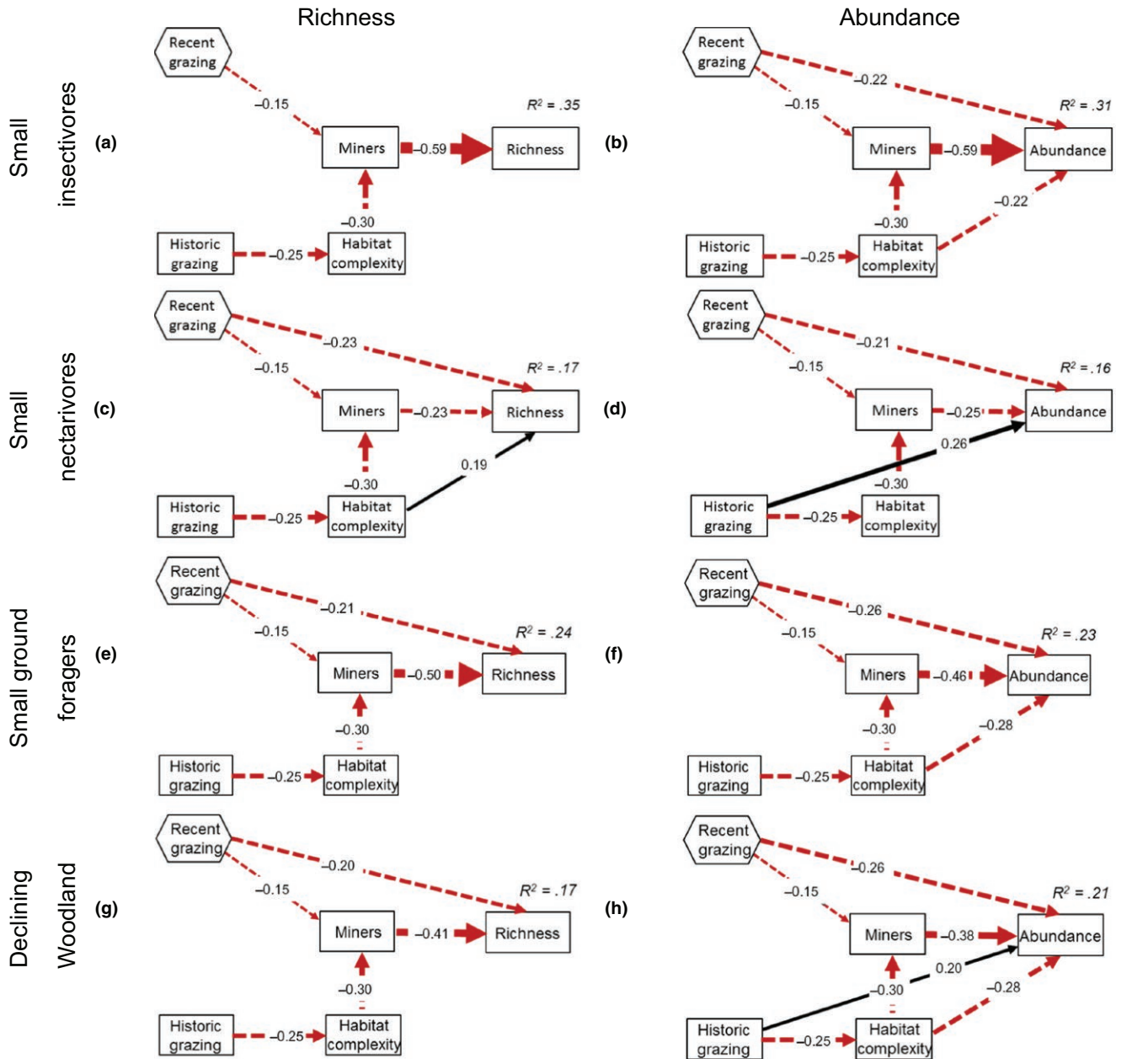

FIGURE 3 Structural equation model of the direct and indirect effects of historic and recent grazing, habitat complexity and miner abundance on richness and abundance of four small bird groups (a–h). Standardised path coefficients, superimposed upon the arrows, are analogous to partial correlation coefficients, and indicative of the effect size of the relationship. Continuous and dashed arrows indicate positive and negative relationships, respectively. The width of arrows is proportional to the strength of path coefficients. The proportion of variance in richness or abundance explained by the model is shown as R^2. $\chi^2 = 1.25$, $df = 1$, $p = .264$, RMSEA = 0, Bootstrapped $p = 1.0$ [Colour figure can be viewed at wileyonlinelibrary.com]

hypothesis and the notion that patch size and complexity define the ecosystem domain of a subset of declining woodland birds (Watson et al., 2001). Our model suggests a direct link between historic grazing and vegetation complexity, and, while the effect of miners on small birds is relatively well known, the links with livestock grazing have not, to our knowledge, been previously documented.

Increased levels of historic grazing tended to reduce the richness and abundance of small birds by reducing the suppressive effect of vegetation complexity on miner abundance (Table 2; Figure 3), consistent with the third hypothesis. Furthermore, this indirect suppressive effect intensified with increasing miner abundance. The increase in abundance of miners in response to alterations to woodland architecture is thought to be through reductions in tree and shrub cover and density (Davies, Melbourne, James, & Cunningham, 2010) and is consistent with how they respond to thinning and logging (Eyre et al., 2015). In semi-arid woodlands, domestic stock grazing substantially reduces the recruitment and regeneration of many shrub and tree species (Tiver & Andrew, 1997), and in temperate woodlands, livestock grazing alters

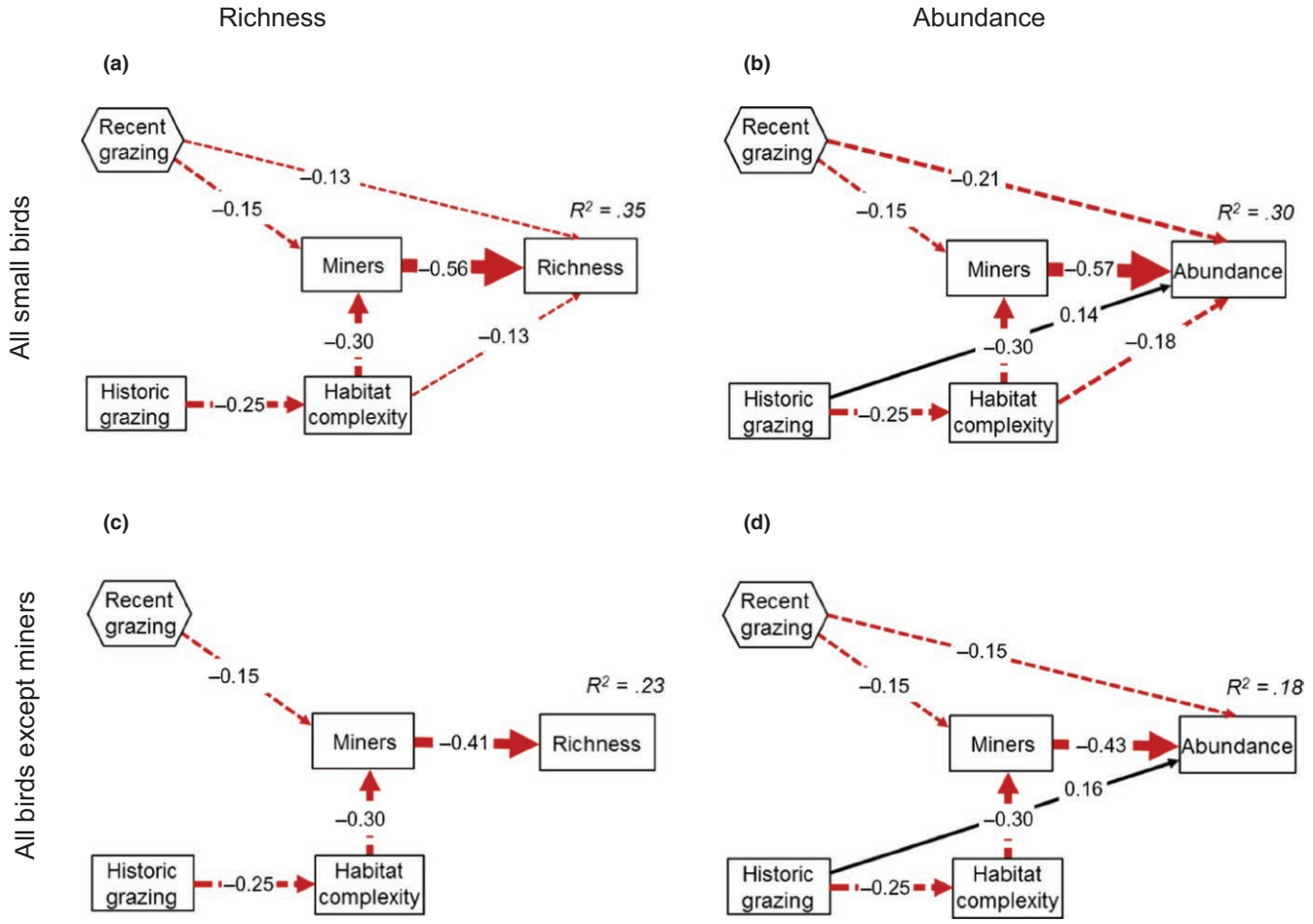

FIGURE 4 Structural equation model of the direct and indirect effects of historic and recent grazing, habitat complexity, and miner abundance on richness and abundance of small birds (a, b) and all birds other than miners (c, d). Standardised path coefficients, superimposed upon the arrows, are analogous to partial correlation coefficients, and indicative of the effect size of the relationship. Continuous and dashed arrows indicate positive and negative relationships, respectively. The width of arrows is proportional to the strength of path coefficients. The proportion of variance in richness or abundance explained by the model is shown as R^2. χ^2 = 1.25, df = 1, p = .264, RMSEA = 0, Bootstrapped p = 1.0 [Colour figure can be viewed at wileyonlinelibrary.com]

the floristic composition and structural diversity of woody plants (Prober & Thiele, 2005). We did not explicitly test the link between grazing and the vegetation complexity. Based on *a priori* information and our collective knowledge, we believe that historic livestock grazing is strongly implicated (e.g. Crisp & Lange, 1976; Soliveres & Eldridge, 2013; Watson, Thomas, & Fletcher, 2007). We acknowledge, however, that factors other than historic grazing could also contribute to the decline in complexity and changes in bird abundance. Bird richness and abundance could respond to short-term shifts in weather patterns such as large La Nina events (Recher & Davis, 2014), but these effects would be consistent across the study area. Indeed, studies of changes in vertebrate richness at regional scales indicate that forest structure and productivity are stronger drivers of bird richness than climate (Coops, Rickbeil, Bolton, Andrew, & Brouwers, 2017).

The density of livestock tracks, our measure of historic livestock grazing, has been used as a surrogate for the long-term use of sites by livestock (Lange, 1969; Pringle & Landsberg, 2004). The decision to use track density as a grazing surrogate is predicated on the fact that a greater density and depth of tracks should reflect longer periods of use by livestock (Pringle & Landsberg, 2004), particularly in the past. Livestock use the same pathways to access water over many years thus the size and depth of their tracks represent a signature of long-term livestock usage related to livestock type, density and behaviour (Pringle & Landsberg, 2004). Reductions in the structural complexity of woody vegetation therefore reflect a long history of grazing (Tiver & Andrew, 1997).

The density of miners have been shown to be greater in areas with moderate to heavy grazing by feral herbivores (Maron & Kennedy, 2007) and heavy grazing by livestock (Howes & Maron, 2009; Martin & McIntyre, 2007). Conversely, miner density has been shown to be negatively correlated with grazing intensity (Jansen & Robertson, 2001), although in that study the effects of grazing could have been confounded by tree clearing, as the heavily grazed sites were also open farmland. Woinarski and Ash (2002) found contrasting responses of miners to grazing, with noisy miners less abundant at grazed sites and its congener, the yellow-throated miner, more abundant at grazed sites. However, none of these studies attempted to separate recent

TABLE 2 Standardised total effects of historic grazing, recent grazing, vegetation complexity and miner abundance on richness and abundance of all birds, all small birds and specific bird groups

Bird groups	Historic grazing	Recent grazing	Vegetation complexity	Miners
Bird richness				
All birds (excl. miners)	−0.18	0.02	0.25	−0.41
All small birds	−0.16	−0.08	0.21	−0.56
Small insectivores	−0.17	−0.03	0.18	−0.59
Small ground foragers	−0.05	−0.14	0.03	−0.50
Small nectarivores	−0.09	−0.23	0.26	−0.23
Declining woodland species	−0.02	−0.13	−0.12	−0.41
Large ground foragers	0	0.23	−0.10	0.45
All large birds (excl. miners)	−0.04	0.19	0.06	0.29
Bird abundance				
All birds (excl. miners)	0.10	−0.08	−0.02	−0.43
All small birds	0.06	−0.13	−0.01	−0.57
Small insectivores	−0.02	−0.12	−0.05	−0.59
Small ground foragers	0.03	−0.17	−0.14	−0.46
Small nectarivores	0.18	−0.20	0.22	−0.25
Declining woodland species	0.18	−0.18	−0.17	−0.38
Large ground foragers	0.15	0.13	−0.13	0.51
All large birds (excl. miners)	0.10	0.14	−0.01	0.46

from historical effects of grazing. We found only weak reductions in miner abundance with increasing recent grazing (Figures 3 and 4), but more predictable reductions in the richness and abundance of four small bird groups (small ground foragers, insectivores, nectarivores and declining woodland species) and increases in abundance and richness of large bird groups (Table 2). The mechanism underlying these effects is likely related to reductions in groundstorey cover, particularly dense litter, that lower the habitat complexity for invertebrates, thereby depleting prey items for small birds (Martin & Possingham, 2005). Reduced structural complexity would advantage large-bodied generalist bird species (Martin & Possingham, 2005) that forage predominately on seeds (Ashley, Major, & Taylor, 2009; Eyre, Maron, Mathieson, & Haseler, 2009) such as crested pigeons (*Ocyphaps lophotes*), galahs (*Eolophus roseicapilla*) and large-bodied predatory birds that benefit from improved visibility within a woodland, such as butcherbirds. Grazing also likely reduces the connectivity among foraging patches, increasing patches of bare ground, which would increase the predation risk for small birds foraging across large areas of open ground. Notwithstanding the importance of complexity in our study, the overall effects of miners (standardised total effects) outweighed any effect of complexity, historic or recent grazing, indicating that the overall effect of miners on small bird richness exceeded that of vegetation complexity (sensu Major, Christie, & Gowing, 2001; Robertson et al., 2013).

Our models showed direct negative effects of recent grazing on small bird richness and abundance (Figures 3 and 4). The direct, and therefore unexplained, negative effect of recent grazing on small bird richness could be due to increased cover of bare ground, which is preferred habitat for large ground-foraging granivorous birds but generally not for smaller insectivores (Kutt & Woinarski, 2007), and which increases under heavy grazing (Eldridge et al., 2017). Grazing is also known to affect habitat in ways other than by altering habitat structure, such as changing plant community composition (Landsberg, James, Morton, Muller, & Stol, 2003). Livestock may also influence small bird richness by competing with herbivorous insects, the main food source of small woodland birds, thereby altering both insect and bird abundance (Milchunas, Lauenroth, & Burke, 1998). Furthermore, livestock may affect the richness of small ground-foraging birds by disturbing their breeding activity or by trampling on nests (Popotnik & Giuliano, 2000).

4.3 | Management implications

Our findings are consistent with other studies that showing that small birds benefit from increasing complexity while large birds are often advantaged by open and simple landscapes (Fischer, Lindenmayer, & Montague-Drake, 2008). The importance of habitat complexity for enhancing small birds and reducing invasions by large-bodied birds has important conservation implications for natural resource management agencies. In agricultural landscapes, appropriate conservation strategies should include promoting the use of shrubs in the restoration projects (Hastings & Beattie, 2006) and careful selection of tree species that do not attract large aggressive nectar feeding birds. In pastoral landscapes, allowing the "thickening" of woodlands, which is viewed by some as a sign of a degradation, has been shown to have substantial ecosystem benefits (Eldridge & Soliveres, 2014) including, as our models suggest, supporting greater richness and abundance of small-bodied birds by limiting incursion by miners (Eyre et al., 2015).

Woodlands have been altered significantly by past clearing, thinning and livestock grazing imposing a legacy effect on bird assemblages, with many species continuing to decline even though most of the damage occurred many decades ago (Ford et al., 2001). Our study shows the importance of managing grazing pressure to prevent further loss of woodland complexity to protect small woodland birds from aggressive large bodied birds. There is growing evidence suggesting that the displacement of small woodland birds by large aggressive birds, such as miners has a direct influence on tree health (Maron et al., 2013). The important implications for the persistence of healthy, functional woodlands given the important ecosystem services are provided by small birds. The links among small birds, large aggressive birds and woodland health is deserving of further investigation.

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AUTHORS' CONTRIBUTIONS

J.V., D.J.E., S.K.T. and I.O. conceived and designed the study; J.V., D.J.E., S.K.T. and contractors collected the data; D.J.E., J.V., and S.K.T. analysed the data; J.V. led the writing of the manuscript, and all authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data on grazing and birds are deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.h2s76. Data files: Richness of bird groups, grazing intensity and habitat complexity (Val, Eldridge, Travers, & Oliver, 2018).

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