Spatially and temporally targeted suppression of despotic noisy miners has conservation benefits for highly mobile and threatened woodland birds

Ross Crates[a,*], Aleks Terauds[a], Laura Rayner[a], Dejan Stojanovic[a], Robert Heinsohn[a], Colin Wilkie[b], Matthew Webb[a]

[a] Fenner School, Australian National University, Linnaeus Way, Canberra, ACT, Australia 2601
[b] Australian Vertebrate Pest Management Ltd., Port Macquarie, NSW, Australia

ABSTRACT

Interactive effects of habitat loss and interspecific competition are major threats to global biodiversity. Managing despotic competitors in modified landscapes is a conservation priority, but implementing actions to benefit rare and highly mobile species is challenging. In Australia, overabundance of hyperaggressive noisy miners following woodland fragmentation and degradation is a key threatening process given their impact on songbirds including the nomadic, critically endangered regent honeyeater. Recent studies have found rapid noisy miner re-colonization following their experimental removal, questioning the efficacy of miner removal as a conservation measure. We estimated the relative habitat saturation of noisy miners at a hotspot of threatened bird diversity. We then experimentally removed 350 noisy miners and assessed the effect of this removal on subsequent noisy miner abundance, relative to a control area. We monitored the occurrence of noisy miners near regent honeyeater nests and modelled the effect of noisy miner removal on songbird populations. Noisy miner removal significantly decreased noisy miner abundance throughout the breeding season, when 15–18 regent honeyeaters nested in the miner removal area. Songbird abundance and species richness increased significantly in the miner removal area, relative to the control area. We provide a rare example of how spatially and temporally targeted preventative action can reduce threats for nomadic and highly threatened species during breeding and prevent ongoing avian diversity loss more broadly.

1. Introduction

Interactive effects of habitat loss and interspecific competition are major and ongoing threats to global biodiversity (Byers et al., 2002; Didham et al., 2007). Habitat loss increases niche overlap and subsequent interspecific competition for remaining resources (Scheele et al., 2017). Increases in the abundance of territorial and disruptive generalists or edge specialists (hereafter 'despotic generalists') following habitat loss and fragmentation can cause biotic homogenisation through competitive exclusion of smaller, rare or mobile species from habitat in which they may otherwise persist (Ford et al., 2001; Robertson et al., 2013).

Following habitat modification, the length of time that interspecific competition can affect population trends of co-occurring species is unclear (Didham et al., 2007). This uncertainty is likely because population trends of competing species can change for decades following habitat modification (Didham et al., 2007). In many modified environments, population changes due to interspecific competition are

therefore likely to be ongoing (Sanderson et al., 2006). Even less clear are the circumstances under which interventions to suppress populations of despotic generalists can be successful and cost-effective (Grey et al., 1998; Davitt et al., 2018).

Highly mobile (i.e. nomadic, semi-nomadic or migratory) species pose unique challenges for conservation because predicting where and when to implement applied conservation action is difficult (Runge et al., 2014). Competitor suppression may represent wasted investment if mobile species do not subsequently occupy that location, or if competitors recolonise shortly afterwards (Stojanovic et al., 2014). Meanwhile, at locations mobile species do occupy, threats from despotic competitors continue unabated. Difficulties predicting when and where mobile species will settle, and associated risk of wasting conservation resources means these species are under-conserved and disproportionately threatened globally (Webb et al., 2014; Cottee-Jones et al., 2015). Nonetheless, competitor suppression is most likely to benefit threatened, mobile species when preventative action is taken at times and locations when both species are present, but before the

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negative impacts of despotic generalists have fully manifested (Cooney, 2004; Crates et al., 2017a; Leung et al., 2002; Pluess et al., 2012).

In southeast Australia, widespread and ongoing vegetation clearance has led to extreme fragmentation of lowland woodland communities (Bradshaw, 2012; Tulloch et al., 2016). The noisy miner *Manorina melanocephala*, a medium sized (~63 g), native generalist honeyeater occupies sparsely-vegetated habitats and has benefitted greatly from habitat fragmentation and degradation (Maron, 2007; Piper and Catterall, 2003). Noisy miners are sedentary cooperative breeders and establish colonies that aggressively exclude smaller-bodied songbirds (passerines, order Passeriformes) from potential breeding habitat (Piper and Catterall, 2003). The presence of even small numbers of noisy miners during breeding risks decreasing reproduction of co-occurring species through nest destruction or disturbance (Thomson et al., 2015; Crates et al., in press). Severe woodland clearance and noisy miner invasion interact to homogenise bird communities via population declines of threatened woodland specialists (Ford et al., 2001; Mac Nally et al., 2012). The noisy miner is therefore listed as a key threatening process under biodiversity legislation and development of methods to reduce their impact on avian diversity is an urgent conservation priority (Threatened Species Scientific Committee, 2014).

Recent studies have experimentally removed noisy miners to assess the viability of culling as an avian conservation measure (Davitt et al., 2018; Beggs et al., in review). A common result of these studies is rapid noisy miner recolonization, often within days, with minimal decrease in miner abundance or increase in songbird abundance (Davitt et al., 2018; Beggs et al., in review). Since earlier studies found songbird populations increased following experimental miner removal (Grey et al., 1998), the factors determining the success of noisy miner removal for avian conservation remain unclear. Here we build on recent work by experimentally removing noisy miners from a known breeding site of the critically endangered and nomadic regent honeyeater *Anthochaera phrygia*. Regent honeyeaters (contemporary population 350–500, Kvistad et al., 2015) are disproportionately impacted by the ongoing spread of noisy miners because lowland woodland clearance has led to extensive overlap between the two species' remaining breeding habitat throughout their 600,000 km^2 range (Commonwealth of Australia, 2016; Ford et al., 2001; Ford, 2011). Where they co-occur, regent honeyeaters compete with noisy miners and other large honeyeater species for nectar and invertebrates (Ford, 1979). Increases in noisy miner abundance over the past two decades may have contributed to a decrease in regent honeyeater nesting success over this period (Crates et al., in press). Challenges associated with the regent honeyeater's small population size, vast range and irregular breeding locations have constrained attempts to implement targeted actions such as competitor suppression to aid population recovery.

We aimed to assess the effectiveness of noisy miner suppression as a means of; 1) reducing noisy miner abundance; 2) preventing and reducing competition from co-occurrence of noisy miners and regent honeyeaters during nesting; and 3) increasing songbird abundance and species richness. Based on the absence of potential source habitats for noisy miners nearby, we predicted that noisy miner removal would lead to a sustained reduction in their abundance, which would prevent their co-occurrence with any breeding regent honeyeaters. We also predicted that songbird diversity and species richness would increase following miner removal, relative to the control area.

2. Methods

2.1. Study location

The study was conducted in woodland surrounding a 7.75 km stretch of the Goulburn River in the Greater Blue Mountains, New South Wales, Australia (Fig. 1). This location is typical of remaining regent honeyeater breeding habitat, with largely cleared agricultural river flats varying in width from 5 to 400 m. Regent honeyeaters breed on lower

slopes and valley floors with remnant patches of box-gum *Eucalyptus* spp. woodland and riparian gallery forest (Crates et al., 2017b; Crates et al., in press). We considered that all potential regent honeyeater breeding habitat was also potential habitat for noisy miners, as these vegetation communities were never > 200 m from a habitat edge (Piper and Catterall, 2003). Surrounding the cleared river flats is largely continuous dry shrubby woodland. In contrast to many areas within the regent honeyeater's range, including the study areas of Davitt et al. (2018) and Beggs et al. (in review), the heavily-forested matrix surrounding the study location is unsuitable for noisy miners, which are rare in the surrounding area (Maron, 2007, Fig. 1). In November 2016, a range-wide regent honeyeater monitoring program detected 4 regent honeyeater pairs breeding within the study location, all of which were frequently observed aggressively defending nests from co-occurring noisy miners (Crates et al., in press).

2.2. Pre-removal bird surveys

During the week commencing 1st August 2017, 189 monitoring sites were established within the treatment and control areas (145 treatment sites and 44 sites control sites, Fig. 1). Although multiple treatment and control areas would have been desirable, the experimental design was determined by external factors including cost, the number of miners that could be removed under licence and the known distribution of breeding regent honeyeaters. Each monitoring site was a point count of the surrounding 50 m radius centred on a fixed location. Monitoring sites were spaced at least 140 m apart, firstly to account for fine-scale variation in noisy miner occupancy, habitat characteristics and associated effects on songbirds (Piper and Catterall, 2003) and second to maximise detection of regent honeyeaters given their small breeding territories (Crates et al., 2017b). During each site visit, maximum counts of noisy miners and other songbirds within each site during a 5-minute survey period were recorded. Adaptive sampling was used to add sites adjacent to those occupied by noisy miners, oriented towards the woodland interior until miners were no longer detected (Smith et al., 2004; Maron, 2007). Each site was visited twice during a 5-day period from 3–7th August 2017, prior to the removal of noisy miners. Detection probability of noisy miners ($p = 0.82$) and other songbirds including the regent honeyeater ($p = 0.59$) using this survey design have been shown previously to be high (Crates et al., 2017b).

2.3. Noisy miner removal

Noisy miners were removed from 430 ha of woodland within the treatment area by two licenced marksmen over a 5-day period commencing 8th August 2017. This date was specifically chosen to be as close as possible to, but before the potential arrival of any regent honeyeaters to the location (Ford et al., 1993; Crates et al., 2017b). Noisy miner calls were broadcast (Pizzey and Knight, 2014) from portable speakers to attract miners, which were subsequently removed from the treatment area using 2×12-gauge shotguns and size 8 shot. The treatment area was divided into 4 sections of approximately equal size and miners were removed via a daily unstructured search of each section. On the fifth day, a follow-up sweep of the entire treatment area was conducted until dusk to maximise the number of miners removed.

2.4. Post-removal bird surveys

Repeat site visits were made to all monitoring sites over 3 sets of 6 day periods, commencing 2 days, 1 month and 3 months after miner removal. As per pre-removal surveys, maximum counts of all songbirds detected during each repeat 5-min site visit were recorded.

2.5. Regent honeyeater monitoring

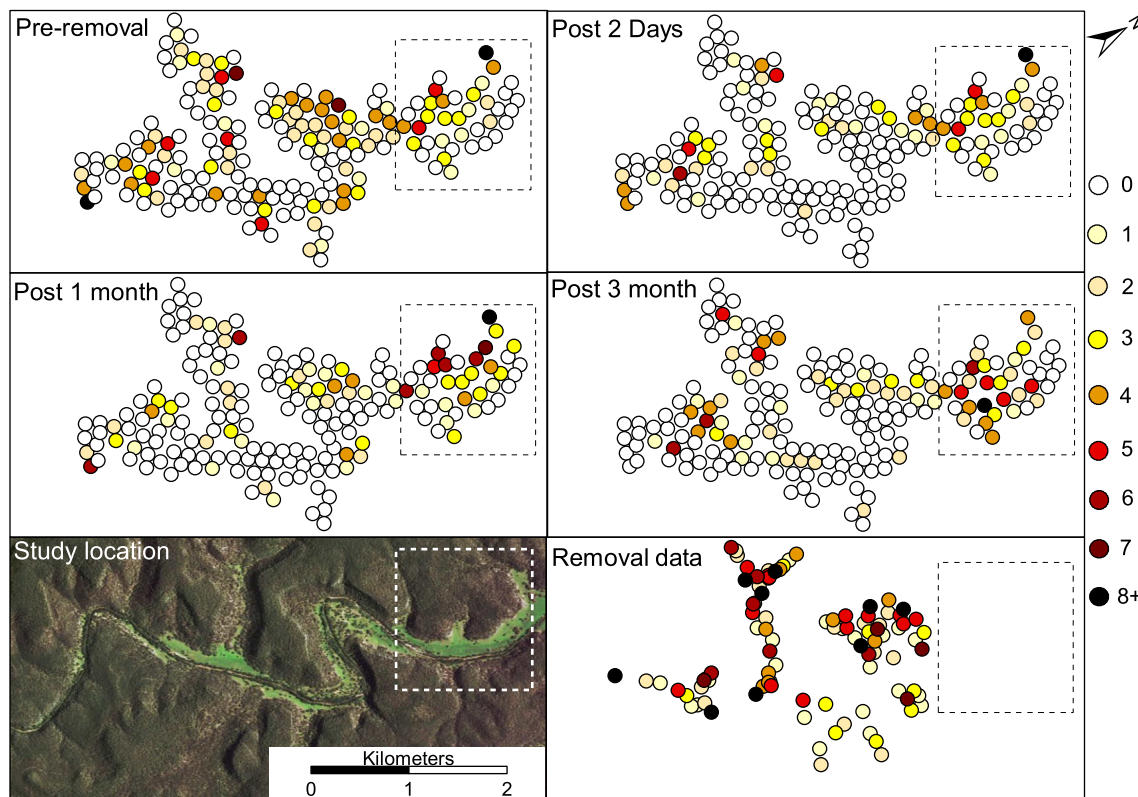Nesting activity of all regent honeyeaters detected (visibly or

Fig. 1. Spatial distribution of monitoring sites at the Goulburn River study site, New South Wales, Australia. Colour shading represents the maximum count of noisy miners detected across repeat site visits at each time period, as defined in legend to right. Dashed polygon denotes control sites. Removal data shows locations within treatment area from where noisy miners were removed (not constrained to within monitoring sites).

audibly) at the study location during bird surveys or opportunistically was monitored every 2–7 days by a single observer (see Crates et al., in press). Each active regent honeyeater nest was observed for ten minutes during each visit from a distance of > 50 m, to determine whether noisy miners and regent honeyeaters co-occurred during nesting (i.e. if miners were observed within 50 m of an active regent honeyeater nest) and any aggressive interspecific interactions were recorded.

2.6. Statistical analysis

To estimate the extent to which the study location was saturated with noisy miners prior to their removal, a centred and scaled principal component analysis (PCA) was implemented using 'factoextra' v1.0.5 (Kassambara and Mundt, 2017). The PCA included all habitat and vegetation covariates that were predicted to potentially influence noisy miner presence or abundance (Table 1). The first two principal components (cumulatively explaining 26.1% of total variation) were plotted and grouped by pre-removal noisy miner presence/absence at each site using 'ggfortify' v0.4.3 (Tang, 2018). The 95% ellipsis was fitted to quantify the 'effective niche space' of noisy miners within the study location. The relative saturation of the study location with noisy miners was estimated by calculating the proportion of monitoring sites within the 95% niche space (i.e. potential noisy miner habitat) where noisy miners were detected during pre-removal surveys.

Habitat covariates were checked for multicollinearity, but no pairs had a Pearson's $r > 0.6$. To account for variation in tree species composition, a second centred and scaled PCA was implemented including the percentage cover of each tree species present within each monitoring site. The first component, explaining 11.1% of total variation, was included in bird models as 'vegetation composition' (Fig. S1).

2.7. Noisy miner models

To assess the relative impact of noisy miner removal on their abundance, noisy miner abundance was modelled as a function of habitat covariates, treatment area (hereafter 'treatment,' and time period (hereafter 'period', Table 1). Modelling frameworks included general linear models (GLMs, using 'MASS' v7.3-50, Ripley, 2018) and generalised additive models (GAMs, using 'mgcv' v1.8-23, Wood, 2018). Given the clear spatial structure in the noisy miner data, spatial location was included as a smoothed bivariate term $s(Lat/Long)$ to account for the spatial autocorrelation (sensu Webb et al., 2014). The appropriate level of smoothing was selected using the *mgcv* default settings and cross validation. GLMs and GAMs were fitted with negative binomial or Poisson distributions, both with a log-link. Analysis of residuals and comparison of AICc values for the 4 model types indicated that GAMs with a Poisson distribution and including the bivariate spatial term were best suited to noisy miner data (Wood, 2017). Overall goodness of fit was assessed using % of deviance explained and R^2. A global model was first fitted including all habitat covariates, an interaction term 'TREATMENT × PERIOD' and $s(Lat/Long)$. Package 'MuMIn' v1.40.4 (Bartoń, 2018) was used to rank all models derived from the global model by AICc. Model averaging was implemented on all models with Akaike weight (W_i) > 0.1 to obtain averaged beta coefficients for each covariate and relevant interaction terms (Burnham and Anderson, 2002). Goodness of fit of the most parsimonious GAM was assessed using function *gam.check* in 'mgcv' and correlograms of Moran's I to test for spatial autocorrelation of residuals using package 'ncf' v1.2–5 (Bjornstad, 2018).

2.8. Songbird models

To assess songbird responses to noisy miner removal, the same

Table 1

Description of site-level covariates tested in models of noisy miner abundance and the abundance and diversity of other songbirds before and after experimental noisy miner removal.

Covariate	Description	Justifying citation
Tree cover	Estimated % canopy cover > 4 m to nearest 5%.	Maron et al. 2007
Shrub cover	Estimated % cover of vegetation of height 30 cm–1.5 m to nearest 5%.	Val et al., 2018
Grass cover	Estimated % ground cover comprised of grass to nearest 5%.	Val et al., 2018
Mid-storey	Estimated % cover of vegetation height 1.5–4 m to nearest 5%.	Maron et al., 2013
Mistletoe	Number of clumps of live mistletoe grouped into none (0), 1–2 plants (1), 3–5 plants (2), 6–10 plants (3), 10–15 plants (4), > 15 plants (5).	Watson and Herring, 2012
Woody debris	Amount of coarse woody debris present in survey area, grouped into none (0), light (1), moderate (2), extensive (3), very extensive (4).	Mac Nally et al., 2001
Large old trees	Number of trees present within each site with a diameter at breast height > 80 cm.	Crates et al., 2017b
Stand age	Estimated mean age of trees to nearest 5 years.	Law et al., 2014
Flower	Eucalypt and mistletoe flower score of none (0), low (1), moderate (2), high (3). Included in saturated models as an interaction with period to account for temporal changes in flower location and abundance. Flower considered a proxy for nectar abundance.	Mac Nally and McGoldrick, 1996; Crates et al., 2017b
Vegetation composition	Principal component based on proportion of all tree species present within each monitoring site, estimated to nearest 5%.	Maron et al., 2011; Grey et al., 1998
Noisy miner	Maximum count of noisy miners across repeat site visits at each time period. Implemented in models of songbird diversity.	Maron et al., 2013; Mac Nally et al., 2012; Piper and Catterall, 2003
Treatment	2 - level factor- noisy miner removal site or control area.	Davitt et al., 2018
Period	4 - level factor- pre noisy miner removal, 2 days, 1 month and 3 months post noisy miner removal.	Davitt et al., 2018; Grey et al., 1998; Beggs et al., in review
Location	WGS 84 decimal latitude/longitude, modelled as a smoothed bivariate term.	Webb et al., 2014

modelling procedure was repeated using songbird abundance (maximum count of each species) and species richness (sum of species detected) as response variables. Site-level abundance metrics were calculated as the maximum count of each species across repeat site-visits at each time period, summed across all relevant species. Site-level species richness indices were the same as those for abundance, replacing count data with binary presence-absence. Analysis of residuals and AICc values indicated GAMs with a negative binomial distribution, and a smoothed bivariate spatial term, were the best fit to the songbird data. Songbird abundance and species richness GAMs were first fitted for all species and subsequently for a set of functional groups therein (Table S1). Functional groups were defined based on factors known or predicted to affect bird abundance at monitoring sites in response to changes in noisy miner abundance, such as body size (Mac Nally et al., 2012) and residency status.

The effect of noisy miner removal on songbird abundance and species richness was examined in two ways: First, GAMs were fitted to all data with a TREATMENT × PERIOD interaction term, as per noisy miner models described above. The effect size and significance estimate of this interaction term were assessed to examine the effect of noisy miner removal on songbird abundance and species richness, relative to the control area. Second, GAMs were fitted with a NOISY MINER ABUNDANCE × PERIOD interaction term on only the monitoring data from treatment area (i.e. excluding data from control area). This was designed to assess changes in the direct effect of noisy miner abundance on songbird abundance and species richness at each time period, avoiding a 3-way interaction term of NOISY MINER ABUNDANCE × PERIOD × TREATMENT. All songbird abundance and richness metrics were calculated excluding noisy miner data. All statistical analyses were implemented in R v3.4.3 (R Core Team, 2017).

3. Results

3.1. Statistical analyses

Model diagnostics of the most parsimonious GAMs confirmed that they were an appropriate model choice in each case. Summary statistics and tests for spatial autocorrelation indicated that the spatial term in the GAMs had successfully accounted for almost all of the spatial structure in the data (Fig. S1).

3.2. Noisy miner abundance

Noisy miners were initially detected at 93/187 monitoring sites. Pre-removal mean noisy miner density was 1.85 (± sd = 0–2.3)/ha at occupied sites. Principal component analysis suggested noisy miners had not saturated suitable habitat within the study location prior to their removal, as miners were not detected at 40% of monitoring sites falling within their niche space (Fig. 2).

Noisy miner abundance was significantly and negatively associated with shrub cover, mistletoe abundance, average tree (stand) age and the vegetation index, and positively associated with grass cover (Tables 2 and 3, Fig. S2). They tended to occupy sites dominated by tree species including rough-barked apple *Angophora florubunda*, river she-oak *Casuarina cunninghamii*, yellow box *Eucalyptus melliodora* and grey gum *E. punctata*. (Table 3, Fig. S2).

A total of 350 noisy miners were removed from the treatment area (Fig. 1). Noisy miner removal led to a 40–45% reduction in their
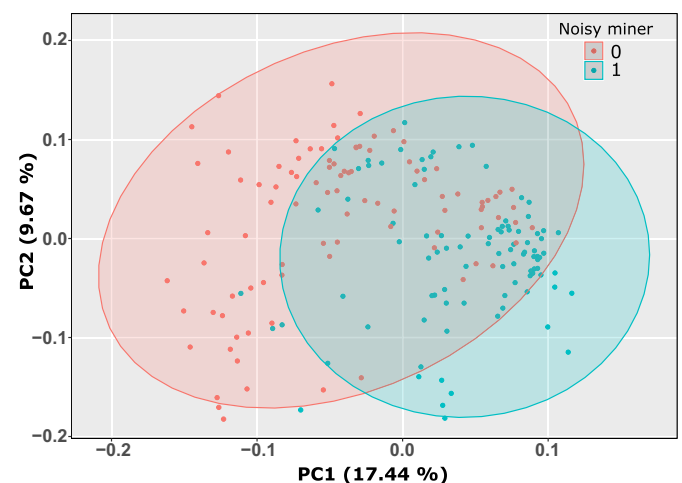

Fig. 2. Ordination scatter plot of principal component analysis (PCA) of site-level habitat covariates at monitoring sites within the Goulburn River study site. Points denote the habitat composition as defined by the PCA of each monitoring site. Blue ellipsis effectively denotes 95% noisy miner 'niche space' within the study site. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Best (lowest AICc, Akaike weight > 0.1) generalised additive models of noisy miner abundance before and after their experimental removal from the Goulburn River study site, New South Wales, Australia. Goodness of fit metrics for top model: $R^2 = 0.471$, deviance explained = 49.7%.

Model	DF	AIC	ΔAIC	w_i
Grass + Mid storey + Period + s(Lat,Long) + Shrub + Stand age + Treatment + Tree + Period * Treatment	40.18	1766.47	–	0.45
Grass + Mid storey + Mistletoe + Period + s(Lat,Long) + Shrub + Stand age + Treatment + Tree + Period * Treatment	41.39	1767.63	1.16	0.25
Grass + Mid storey + Period + Vegetation composition + s(Lat,Long) + Shrub + Stand age + Treatment + Tree + Period * Treatment	41.18	1768.14	1.67	0.19
Grass + Mid storey + Mistletoe + Shrub + Stand age + Period + Treatment + Tree + Vegetation composition + Period * Treatment	42.36	1679.22	2.75	0.11

Table 3

Conditional model-averaged beta coefficients of covariates included in top ranked (Akaike weight > 0.1) generalised additive models of noisy miner abundance over the course of a breeding season at the Goulburn River study site, New South Wales. Significant effects defined as p < 0.05 highlighted in bold.

Covariate	Factor level	B	se	Z	P
(Intercept)		1.890	0.42	4.52	**< 0.01**
Mistletoe		−0.142	0.03	5.04	**< 0.01**
Shrub		−0.034	0.01	6.13	**< 0.01**
Stand Age		−0.017	0.00	4.40	**< 0.01**
Period[1]	Post 2 day	−0.096	0.16	0.62	0.54
Period	Post 1 month	0.056	0.15	0.37	0.71
Period	Post 3 month	0.077	0.15	0.52	0.60
Treatment[2]		−0.768	0.26	2.93	**< 0.01**
Tree cover		−0.010	0.00	3.31	**< 0.01**
Vegetation species		−0.341	0.04	8.36	**< 0.01**
Period * Treatment[3]	Post 2 day	−0.820	0.21	3.94	**< 0.01**
Period * Treatment	Post 1 month	−0.870	0.20	4.34	**< 0.01**
Period * Treatment	Post 3 month	−0.744	0.20	3.81	**< 0.01**
Grass		0.007	0.01	2.69	**0.01**
Mid-storey		−0.014	0.01	2.40	**0.02**
			edf	χ^2	P[4]
S(Lat,Long)			27.36	242.3	**< 0.01**

[1]Relative to pre-noisy miner removal. [2] relative to control site. [3] relative to pre-noisy miner removal and control site. [4]Approximate significance of smoothed spatial term.

presence and a 21% decrease in their mean abundance at occupied sites within the treatment area (Figs. 1 and 3), which lasted the duration of the study (Figs. 2 and 3, Table 3). By contrast, noisy miner abundance increased by 16% at the control area over the season (Figs. 1 and 3).

Relative to the control area and their pre-removal abundance, there was a significant negative effect of TREATMENT × PERIOD interaction on noisy miner abundance over all time periods (Figs. 2 and 3, Table 3). This effect was strongest at 1 month, and weakest at 3 months post-noisy miner removal (Table 3).

3.3. Regent honeyeaters

The first regent honeyeaters were detected at the study site 2 days after miner removal ceased. Between 15 and 18 regent honeyeaters were detected during the study, potentially representing 8–10% of the global effective population (Kvistad et al., 2015). Whilst one colour marked individual observed in 2016 returned to breed at the treatment site in 2017, at least three others were not detected in 2016, having been colour marked in previous years > 100 km away (R. Crates, unpublished data). All regent honeyeaters were located within the treatment area, as were 6 associated nesting attempts. Nests were located in two aggregations, one of 4 nests in the centre of the treatment area where no co-occurrence with noisy miners was observed, and a second of two nests near the northern boundary of the treatment area. Although noisy miners co-occurred with regent honeyeaters at this second aggregation, competitive interactions between noisy miners and these two breeding pairs were only observed during 2/7 nest observation bouts. Three nests (including one co-occurring with noisy miners) were successful, together fledging 5 juveniles.

3.4. Songbird response

Sixty-six songbird species were detected at monitoring sites, including 8 species with a population status of 'vulnerable' or higher (Table S1). Whilst songbird abundance increased following the removal
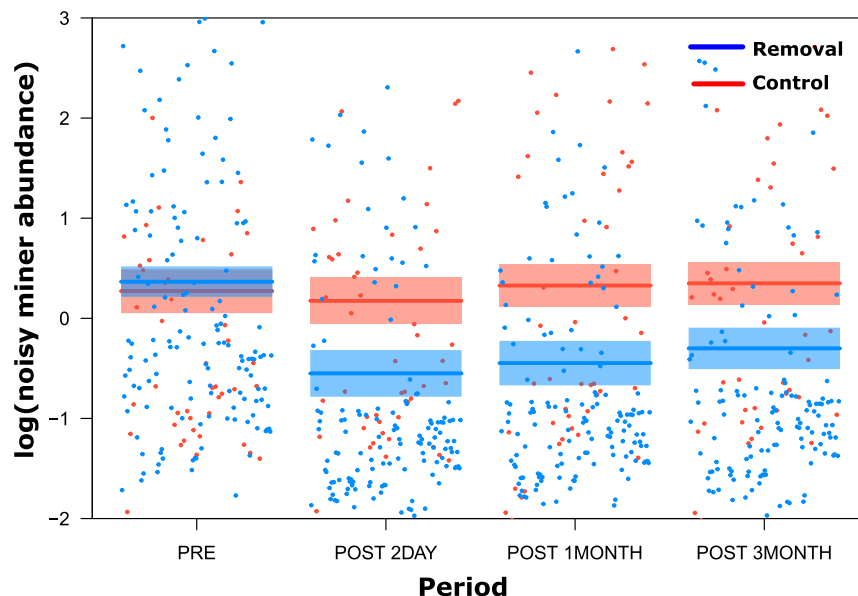

Fig. 3. Relative changes in noisy miner abundance (mean ± 95% CI) at treatment and control areas over the study period. Estimates derived from conditional model-average of generalised additive models with Akaike weight > 0.1. Points denote partial residuals.

Table 4

Best generalised additive models (GAMs) of the effect of noisy miner removal on temporal changes in total songbird abundance and species richness at the Goulburn River study site, New South Wales. Associated beta coefficients for Treatment × Period derived from conditional average of models with Akiaike weight > 0.1. Significant effects defined as $p < 0.05$ highlighted in bold. Best models for functional groups are shown in Table S2 and beta coefficients for other covariates in best models are presented in Table S3. Goodness of fit metrics for abundance and species richness models, respectively: $R^2 = 0.45$ and 0.49, deviance explained = 50.6% and 50.9%.

Response metric	Best model			TREATMENT × PERIOD term				
		ΔAICc[1]	w_i	Level	β	SE	Z	P
Abundance	Period + Flower + Shrub + Stand age + Treatment + Mistletoe + s(Lat/Long) + Period * Treatment	−0.1	0.3	Post 2 days	0.12	0.18	0.66	0.51
				Post 1 month	**0.42**	**0.18**	**2.36**	**0.02**
				Post 3 month	0.22	0.17	1.29	0.20
Species richness	Period + Flower + Shrub + Stand age + Treatment + Mistletoe + s(Lat/Long) + Period * Treatment	−0.15	0.28	Post 2 days	0.13	0.16	0.8	0.42
				Post 1 month	**0.40**	**0.16**	**2.5**	**0.01**
				Post 3 month	0.22	0.15	1.4	0.15

[1] ΔAICc presented as difference between best and second best models, hence negative values.
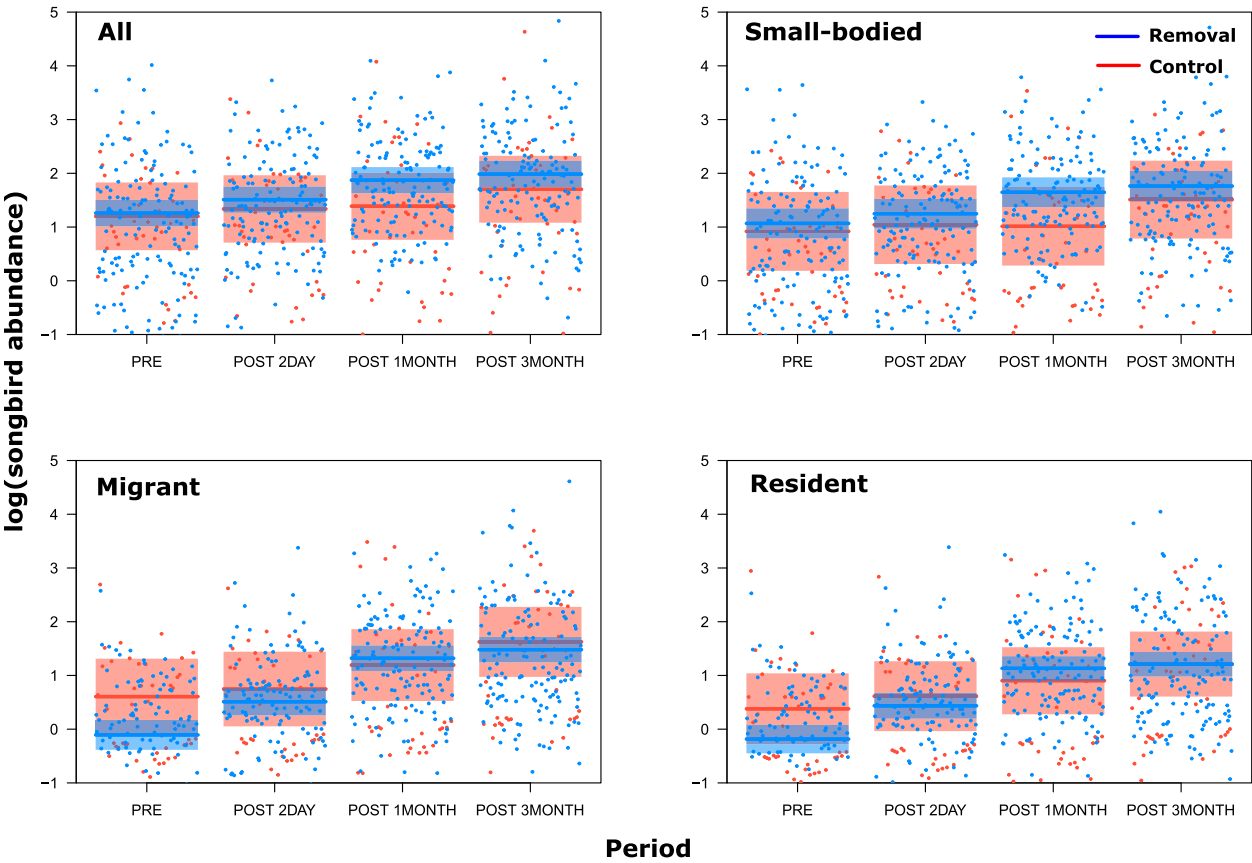

Fig. 4. Relative temporal changes in songbird abundance at noisy miner treatment and control area on the Goulburn River, New South Wales. Estimates derived from conditional model average of models with Akaike weight > 0.1. Points denote partial residuals. Further results shown in Table S2.

of noisy miners in the treatment and control areas (Table 4, Fig. 4), the increase was significantly greater in the treatment area than the control area at 1 month after miner removal (Table 4). Increases in abundance were similar across all functional groups (Fig. 4), suggesting that the positive effect of miner removal on songbird abundance was not solely driven by increases in small-bodied species or the subsequent return of summer migrants in spring. Effects of miner removal on songbird species richness were broadly similar to those for songbird abundance, suggesting that increases in species richness were not due to increases in the abundance of a small number of resident species (Table S2, Fig. S3). Overall, the effect of miner removal on songbird abundance and species richness was significant but relatively small (Fig. 4). Habitat covariates, including mistletoe and flower abundance, shrub and mid-

storey cover and stand age also positively influenced songbird abundance and diversity (Tables 4 and S2). As with the previous models, the smoothed spatial location term used to account for spatial auto-correlation was also significant.

Within the treatment area, noisy miner removal led to a significant reduction in the negative effect of noisy miner abundance on overall songbird abundance. Although the effect was significant just 2 days post- miner removal, it was greatest at 1 month and 3 months post miner removal (Fig. 5).

4. Discussion

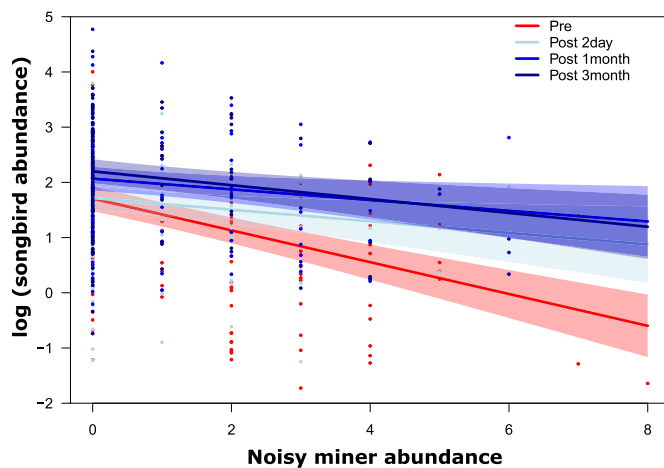Effective management of despotic generalists is critical to

Fig. 5. Effect of noisy miner abundance on overall songbird abundance before, 2 days, 1 month and 3 months following noisy miner removal within the treatment (removal) area at the Goulburn River, New South Wales. Points denote partial residuals.

minimising biodiversity losses following habitat loss and fragmentation (Sakai et al., 2001). For the conservation of threatened and highly mobile species, robust evidence is required to ensure that competitor suppression is implemented using methods that obtain the greatest biodiversity benefits for the smallest financial and ethical costs (Beggs et al., in review). Here we report a rare contemporary example of the successful reduction in abundance of the despotic noisy miner. Preventative noisy miner suppression provided relief from a known source of nesting failure for the critically endangered and nomadic regent honeyeater at an ecologically relevant time and location. Noisy miner suppression also increased abundance and species richness of the broader songbird community.

Consistent with previous studies, noisy miners occupied sites with minimal shrub cover and young trees (Piper and Catterall, 2003; Mac Nally et al., 2012). Noisy miners were positively associated with a particular tree species assemblage (Table 3, Fig. S2), potentially due to the high abundance of lerp (*Psyllidae* sp.) associated with these species (Woinarski and Cullen, 1984). Principal component analysis suggested the noisy miner population had not yet saturated the habitat available to them within the study site, prior to their removal (Fig. 1). Pre-removal noisy miner density was 25–110% lower than at the locations of other recent studies (Davitt et al., 2018; Beggs et al., in review) and noisy miner abundance increased by 16% over the breeding season within the control area. Further, 8 threatened species were detected, which have already vanished from many parts of their former range where noisy miners are now ubiquitous (Ford et al., 2001; Ford, 2011).

In contrast to recent studies and despite lower removal effort (Davitt et al., 2018; Beggs et al., in review), removal of noisy miners here led to a significant and sustained decrease in their abundance within the treatment area. Three factors may have inhibited the success of other recent miner removal experiments. First, removal efforts in these studies were focused in highly fragmented agricultural landscapes where noisy miner abundance has increased in recent decades, facilitating rapid recolonisation (Grey et al., 1998; Davitt et al., 2018; Beggs et al., in review). Second, degraded woodland remnants may no longer represent suitable habitat for specialist songbird species such as the regent honeyeater, and it is possible that no nearby source populations of other threatened species persisted to allow immigration following miner removal (Davitt et al., 2018; Beggs et al., in review). Due to the forested matrix surrounding our study site, noisy miners were uncommon in the wider landscape, minimising the opportunity for removal to be negated by immigration (Fig. 2, Hanski, 1998). A third potentially critical factor is the timing of removal actions (Zavaleta

et al., 2001). We specifically removed noisy miners during the early breeding season, to pre-empt the likely return date of any regent honeyeaters (Crates et al., 2017b). During this period, most noisy miners are settled into breeding territories (Dow, 1978), and opportunities to suppress subsequent population growth by minimising breeding activity is greatest.

Noisy miner suppression reduced, but did not eliminate, co-occurrence with regent honeyeaters during nesting. The presence of miners in the vicinity of two regent honeyeater nests is likely explained by the location of these nests. Pre-removal abundance of noisy miners here was very high, and although > 30 individuals were removed from this location, it is likely some persisted or immigrated from the control site. Given their pre-removal abundance at this location, it is likely that noisy miners would otherwise have excluded regent honeyeaters from settling in this area altogether, or disturbed their reproductive attempt (Mac Nally et al., 2012). The low level of aggressive interaction observed between noisy miners and nesting regent honeyeaters could be explained by removal efforts selectively targeting individuals with the most aggressive behavioural syndrome via their territorial response to call playback (Sih et al., 2004). Alternatively, fragmentation of the social structure of noisy miner colonies could have reduced cooperative aggression in remaining individuals (Davitt et al., 2018). Follow-up removal efforts are required to minimise noisy miner abundance and associated risk to breeding regent honeyeaters and other threatened species.

The effect of noisy miner removal on songbird abundance and richness was significant and positive but relatively small. Noisy miner density at the Goulburn River exceeded a threshold of $0.6\,ha^{-1}$, beyond which miners can diminish songbird abundance and species richness (Thomson et al., 2015). Yet, noisy miners did not occupy all suitable habitat (Fig. 2) and their abundance here was still very low relative to other areas (Thomson et al., 2015; Davitt et al., 2018; Beggs et al., in review). This suggests that miners had not yet, or only recently, reached densities sufficient to diminish the broader songbird community at the Goulburn River (Piper and Catterall, 2003; Beggs et al., in review).

In line with previous studies (Debus, 2008; Watson and Herring, 2012), songbird abundance and species richness were also positively associated with habitat complexity (shrub, mid-storey and mistletoe) as well as stand age and flower abundance (Bennett et al., 2014; Mac Nally and McGoldrick, 1996). Noisy miners were negatively associated with these habitat features, emphasising the potential double benefit of targeted habitat restoration to increase songbird abundance and decrease noisy miner abundance (Debus, 2008; Law et al., 2014).

By identifying critical locations in time and space, our study takes steps towards maximising the cost-effectiveness of targeted noisy miner suppression for conservation of threatened and highly mobile species. Although our study lacked replication at the treatment level, applied management involving lethal actions have an ethical obligation to maximise broader inferences, especially when despotic species are native (Soulé et al., 2005). Future landscape-scale removal experiments could confirm the role of the wider habitat matrix (i.e. forest extent and noisy miner abundance) and removal timing on the success of noisy miner removal actions.

Long-term, repeated removal experiments could also help quantify the importance of preventative action for conserving those species most at risk from ongoing noisy miner invasion (Cooney, 2004; Crates et al., 2017a). Experimental quantification of the importance of early intervention is extremely rare in conservation (see Thompson et al., 2000 for theoretical example). However, such evidence may be critical for justifying and funding actions to conserve the most at-risk species, where causal evidence is not only lacking, but also challenging and time-consuming to obtain (Crates et al., 2017a). For species such as the regent honeyeater, population recovery is unlikely unless the initial cause of population decline, severe habitat loss, is addressed (Caughley, 1994; Crates et al., 2017a). Short term interventions such as noisy miner removal are therefore likely to be essential for minimising interacting

effects on small populations until the time restored and regenerating habitat becomes functional breeding habitat and unsuitable for despotic generalists.

Although effective in the past (Grey et al., 1998; Debus, 2008), recent research suggests high financial costs for low conservation returns makes noisy miner removal uneconomical in agri-environments where habitats are highly degraded, miners are now widespread and threatened species have already disappeared (Beggs et al., in review). Informed by a spatially-extensive monitoring programme to locate regent honeyeaters (Crates et al. in press), we were able to identify a critical breeding area where noisy miners were at relatively low abundance, uncommon in the surrounding matrix and threatened songbird populations persist. Thus, we provide evidence that spatially and temporally targeted competitor suppression can be a viable short term preventative measure to reduce threats for rare and highly mobile species during the critical breeding period. To overcome interacting effects of habitat loss and noisy miner expansion on songbird populations, at-risk diversity hotspots should also be the focus for urgent and large-scale habitat restoration (Didham et al., 2007; Mortelliti et al., 2016). Together, targeted preventative competitor suppression and habitat restoration offers a promising approach to minimise Australia's avian extinction debt.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.10.006.

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