An empirical test of the mechanistic underpinnings of interference competition

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Abstract

Interspecific competition is an essential element of the evolution of species and can strongly influence the abundance and distribution of species. Where competition interacts with anthropogenic habitat modification, this natural ecosystem process can become a threatening process. Understanding the mechanisms behind competition in such cases is essential for the formulation of cost-effective management responses for biodiversity conservation. According to the resource availability hypothesis of competition, interference competition limits access to resources by species vulnerable to such aggression and wastes energy in evasive responses. Studying competition is notoriously difficult, however, empirical evidence of the resource availability theory is limited, and there are few published experimental studies showing such an effect at larger scales. We present the results of a controlled and replicated empirical study of interference competition at a landscape scale. We removed an aggressive, overabundant native bird, *Manorina melanocephala* (noisy miner), whose interference competition is a threatening process for small woodland birds in the highly modified agricultural landscapes of eastern Australia. We monitored foraging and harassment rates of small woodland birds before and after removal to indicate if levels of interference competition changed. Due to unexpected immediate recolonisation, abundance of *M. melanocephala* in treatment sites declined by only 34% relative to control sites. Twenty-four bird species displayed aggressive behaviour towards other birds and 41 bird species were victims of aggression. *Manorina melanocephala* was responsible for 66% of all aggressive interactions. After removal, we recorded a doubling in foraging rate of small woodland birds in treatment compared to control sites. This appears to confirm the resource availability hypothesis of competition. Paradoxically, however, increased foraging was not accompanied by a decline in harassment. Low detection rates of harassment of small woodland birds, combined with the modest reduction in abundance of *M. melanocephala*, make it difficult to draw firm conclusions about the relationship between rates of harassment and rates of foraging.

Introduction

Interspecific interactions such as competition can be a key determinant of the abundance and distribution of species (Case et al. 1974, Darwin 1859, Elton 1927). Through its effect on resource availability, competition can contribute to niche contraction for less competitive species (Chase et al. 2002, Doherty et al. 2018, Kunte 2008). Interference competition occurs where there is a high degree of competitive overlap and resources are economically defendable, hence resources are monopolised by one group through aggressive exclusion of competitors (Brian 1956, Case et al. 1974). This form of competition can have a particularly strong influence on species assemblages when anthropogenic biotic or abiotic changes favour aggressive generalist species. Competition can then become a threatening process for declining species, leading to biotic homogenisation (Robertson et al. 2013, Rooney et al. 2007). Anthropogenic habitat modification is a particularly prevalent form of pressure that entails both biotic and abiotic changes and can transform interference competition into a threatening process (Bennett et al. 2015, Diller et al. 2016, Leseberg et al. 2014, Robertson et al. 2013). Here, we consider the effects of an extreme form of interference competition exerted by an overabundant, hyperaggressive native bird. In combination with habitat modification, this competition has led to homogenisation of avian assemblages at a scale of over one million km^2 (Mac Nally et al. 2012, Maron et al. 2013).

Addressing such threats through habitat restoration is difficult politically and practically (Evans 2016, Hinton et al. 2013, Lindenmayer 2017, Mac Nally 2008). In addition, where biotic and abiotic conditions have been changing in the long term, hysteretic effects mean that removing the primary threat of competition may not ensure reoccupation by declining species (Maron et al. 2013, Suding et al. 2004). This is particularly the case where other competitive species have occupied the niche space vacated by declining species (Doherty et al. 2018, Hinton et al. 2013, Maron et al. 2013). Hence, direct intervention to reduce the abundance of species whose interspecific interactions threaten declining species is a common management response (Diller et al. 2016, Grarock et al. 2014, Kosciuch et al. 2008).

Theory suggests that victims of interference competition have poorer access to resources and waste energy in responding to disturbance (Bechet et al. 2004, Ford 1979, Mac Nally et al. 2005, Moore et al. 2016). If this is the case, then reducing the abundance of the interference competitor should improve resource availability for declining species and reduce the amount of aggression suffered. Studying competition is practically difficult, however, empirical evidence of the resource availability hypothesis is limited, and there are few published experimental studies showing such an effect at larger scales.

We tested the effect of a landscape-scale experimental removal of a hypercompetitive native Australian bird, *Manorina melanocephala* (noisy miner), on foraging and harassment rates of declining small (<63g)

woodland birds. This group is among the most threatened of Australian birds (Barrett et al. 2007).

Manorina melanocephala is a medium-sized honeyeater with a weight of 70 – 80g (Higgins et al. 2001).

It is a sedentary, colonial species whose extreme co-operative territorial aggression affects a wide range of small woodland birds (Maron et al. 2013). Aggressive exclusion of birds from potential habitat by *Manorina melanocephala* is a Key Threatening Process under Australian conservation legislation (Department of the Environment 2014). Impacts occur at *Manorina melanocephala* densities as low as 0.6 birds/ha (Thomson et al. 2015) and across an area of 1.3 million km^2 (Higgins et al. 2001). The combination of the scale of their impact and the intensity of the interference competition they exert makes *Manorina melanocephala* both an environmental problem in urgent need of a solution, and an ideal experimental subject to test the mechanisms underpinning interference competition.

Several ecologists have suggested culling of *Manorina melanocephala* as a management response in some circumstances (Mortelliti et al. 2016, Thomson et al. 2015). Our study therefore has a theoretical and a practical component. We sought to elucidate the ecological processes underpinning the effect of a hyperaggressive competitor on declining bird species and to evaluate the potential for limiting such competition through lethal control of the hyperaggressive species. We used foraging rates and harassment rates as metrics of the intensity of interference competition. We compared these rates for small woodland birds before and after removal of *Manorina melanocephala*. We posed two questions:

1. Does removing an aggressive, overabundant bird reduce interference competition for vulnerable species?

2. Does removing an aggressive, overabundant bird increase foraging rates for vulnerable species?

Based on expert opinion (M. Maron 2016, personal communication) and the evidence of previous removals of *Manorina melanocephala* (Grey et al. 1997, Grey et al. 1998), we predicted that the cull would result in a significant reduction in *Manorina melanocephala* abundance in treatment sites compared to control sites. *A priori*, we posited three possible outcomes for small woodland birds.

i.   A decline in harassment rates and an increase in foraging rates, indicating that removing *Manorina melanocephala* improves resource availability.

ii.   An increase or no change in harassment rates and a decline or no change in foraging rates, indicating compensatory harassment by other bird species when *Manorina melanocephala* are removed.

iii. A decline in harassment rates but no change in foraging rates, indicating that harassment by *Manorina melanocephala* is not the principal source of limited resource availability.

However, due to almost immediate recolonisation of treatment sites by *Manorina melanocephala* after each of two culls, final *Manorina melanocephala* abundance in treatment sites in the post-cull breeding season was higher than expected. Similar compensatory immigration has been reported in a recent cull of *Manorina melanocephala* (Davitt et al. 2018) and other taxa (Grarock et al. 2012, Kierepka et al. 2017, King et al. 2011, Lazenby et al. 2015). Overall, *Manorina melanocephala* abundance in control sites increased by 21% (95% confidence intervals: -0.3%, 47%) and in treatment sites declined by 13% (29%, -6%) (Beggs et al. 2019b). We therefore predicted that any difference in the change in harassment or foraging rates between treatment and control sites would be commensurate with this lower than expected decline in *Manorina melanocephala* abundance.

We also considered two potential complicating factors. First, *Manorina* species are highly social, with a complex co-operative territorial defence system (Arnold 2000, Clarke et al. 1994, Dow 1970) and possible social associations with other species (Fulton 2008). Behavioural changes resulting from replacement of an existing *Manorina* community with new individuals following a cull are therefore possible and this could influence their interactions with other species (Davitt et al. 2018). Second, *Manorina melanocephala* are not the only aggressive species present in this landscape. *Manorina melanocephala* structure species assemblages in the agricultural landscapes in which this study took place, favouring larger, aggressive generalist species (Maron et al. 2013). The study therefore also aimed to discover whether these other aggressive species compensate for any post-cull reduction in harassment by *Manorina melanocephala*.

Material and Methods

Study area
We conducted our experiment from 2015 to 2017 in the adjacent shires of Gundagai (35°03'55.5"S 148°06'18.7"E) and Junee (34°52'11.7"S, 147°35'07.9"E), in the South West Slopes Bioregion of New South Wales, Australia (Figure 1). This region is part of eastern Australia's agricultural belt. More than 85% of the original woodland has been cleared in the region with local losses even higher (Lindenmayer et al. 2005). The ecological value of remnant patches of woodland is affected by fragmentation and degradation through grazing and changed nutrient and fire regimes (Hobbs et al. 1990). 2.28 per cent of the land area of the bioregion is under conservation tenures (OEH 2015). The majority of remnant woodland in the region is on private farmland. Biophysical details of the study region are given in Mortelliti and Lindenmayer (2015).

The study was located within the South West Slopes Restoration Study, a long-term ecological monitoring program conducted by The Australian National University. As part of this program, annual monitoring of birds has been conducted in woodland patches since 2000. Indications are that many small woodland birds have declined whilst *Manorina melanocephala* and larger aggressive generalist species have increased their range and abundance (Cunningham et al. 2008, Mortelliti et al. 2016). More recently, *Manorina melanocephala* abundance appears to be declining in the region (Lindenmayer et al. 2016, Mortelliti et al. 2015).

Experimental design

We selected eight paired patches of remnant or regrowth native eucalypt woodland on seven private mixed arable/grazing farms in the region such that six farms had one pair of patches and one farm had two pairs (Figure 1). Patch size ranged from four to 49ha. Within each patch, we used an existing randomly located 200m marked transect as the central axis of a 2ha study site. We randomly allocated one patch in each pair to treatment or control (Figure 1). Each pair of patches was at least 1142m apart to ensure independence and discourage recolonisation post-cull, based on *Manorina melanocephala*'s published home range of about 200m (Dow 1979). All sites had consistent detection rates of *Manorina melanocephala* of more than 20%.

Habitat factors at both site and landscape scales affect presence of small woodland birds (Cunningham et al. 2014, Montague-Drake et al., 2011, Polyakov et al., 2015). Hence, we chose paired woodland patches based on similar size and vegetation characteristics, using a rapid visual assessment, to account for variance at patch scale. We considered each farm to be a coherent ecological unit with consistent management of woodland patches (Cunningham et al., 2007) and for which the surrounding landscape was largely the same. Mean distance between treatment and control sites was 2224m, (SD = 1710m) so any local variations in productivity due to rainfall were likely to be similar in both treatment and control groups.

We used a BACI (Before-After-Control-Impact) design (Stewart-Oaten et al. 1986) to account for annual variations in environmental conditions that might affect bird behaviour or abundance (Lindenmayer et al. 2011, Tulloch et al. 2016a). We conducted foraging and harassment surveys between October and December in all sites in the pre-cull 2015 breeding season and in the post-cull 2016 season.

Experimental treatment

We conducted the cull of *Manorina melanocephala* in experimental treatment patches using a shotgun in May and June 2016 during the Southern Hemisphere winter, non-breeding, season. We conducted two complete culls at each treatment site. We culled across the whole of each patch and to a radius of 500m where patches abutted potential sources of recolonization such as other woodland patches. We considered culling complete when there was no visual or auditory response by *Manorina melanocephala* to a continuous 45-minute playback of a selection of *Manorina melanocephala* calls. See Beggs et al. (2019b) for full methodology and costings of the cull.

Survey protocols

We conducted eight one-hour surveys of foraging and harassment rates at each site during the breeding season (September – December) before the cull (2015) and in the breeding season following the cull (2016). Post-cull surveys continued up to six months after the cull. The eight repeat surveys were used to eliminate day effects (Field et al. 2002). The observer followed the 200m transect in each site twice in each direction whilst looking and listening for small woodland birds and aggressive interspecific interactions up to 50m either side of the transect. Detection at 40m is considered to be high in forest environments (Mac Nally et al. 2000, Mac Nally et al. 2005). Given minimal understorey and the open structure of the woodland in our study, we assumed high detection rates of birds up to 50m away.

For foraging surveys, on discovering an individual or group of small woodland birds, the observer paused the timer and watched the bird(s) for foraging activity for up to one minute to avoid bias towards conspicuous behaviours. We recorded each foraging observation, whether of a single bird or a group, as one foraging event and also recorded group size. The timer was then restarted and progress resumed along the transect. For harassment surveys, we recorded any aggressive interspecific interaction and noted the species and number of the aggressor and victim along with location (Ground, Air or Canopy), duration, type of interaction (Chase, Supplant, Harassment, Posturing; see Table S1), and the victim's response (Retreat, Leave patch, Hold ground, Fight back). We defined aggressor species as species observed initiating at least one aggressive interaction with another species of bird.

We did not conduct surveys during weather conditions likely to inhibit bird activity or detection, such as strong winds, rain and very high temperatures (O'Connor et al. 1980). We conducted six of the eight annual surveys in the five hours after dawn. Two out of eight were done later in the day with sites surveyed on a rotating basis such that over each season all sites were monitored equally at the different times. Such afternoon surveys have been used on previous studies in eastern Australia (Bennett et al.

2015, Robertson et al. 2014). Most surveys were conducted by the same experienced birdwatcher to minimise observer heterogeneity.

Experimental variables

The aim of the experiment was to explain the impact of the culls of *Manorina melanocephala* on the incidence of interference competition and of foraging by small woodland birds whilst accounting for the influence of other site or landscape variables that might influence the response variables (Table S2). Due to multicollinearity, we excluded woodland extent at 100ha and 10 000ha, using only woodland extent at 1000ha in our models.

General approach to modelling

We constructed generalised linear mixed effects models (GLMMs) of the effects of BACI base variables (Treatment, Phase and Treatment:Phase interaction) and other patch and landscape variables on foraging and harassment rates respectively. Treatment and Phase were binary variables. Treatment had values Treatment (cull) and Control (no cull). Phase had values 0 (pre-cull) and 1 (post-cull). We started with a global model which included BACI base variables plus five landscape- and patch-scale predictor variables (Table S2). We used a Poisson distribution for harassment models and a negative binomial distribution for foraging models as these gave the lowest AIC score. Models had a logarithmic link function and we included Site and Farm as random effects to account for repeated surveys over time (Zuur et al. 2009). We conducted standard diagnostic tests to ensure model assumptions were not violated. All modelling was done in the glmmTMB package (Brooks et al. 2017) in statistical software R, version 3.3.2 (R Core Team 2017).

We used R package MuMIn (Barton 2018) to assess all possible models using all predictor variables, constrained by inclusion of BACI base variables. Model selection was based on lowest Akaike Information Criterion (AIC) score (Burnham et al. 2003).

The purpose of our modelling was to determine if changes in foraging or harassment rates from the pre-cull phase to the post-cull phase were different in treatment compared to control sites. In the BACI design, any such difference is indicated in the Treatment:Phase interaction term. The link function in our models provided the coefficients of predictor variables on the log scale. For simplicity of interpretation, we plot results back-transformed to the non-log scale to give expected numbers of harassment or foraging events with 95% confidence intervals.

Qu1. Does removing an aggressive, overabundant bird reduce interference competition for vulnerable species?

To indicate the amount and direction of aggressive interspecific interactions in this landscape under normal circumstances, we prepared an interaction matrix by cross-tabulating all interactions between aggressor and victim species pre-cull. From this matrix we constructed a chord diagram in R package Circlize (Gu et al. 2014) to show visually the relationships between aggressors and victims. Small woodland birds were victims of harassment in only 41 cases across our two phases and two treatments, thereby limiting our scope for analysis to species level. For the purposes of modelling, we therefore aggregated the total number of harassment events where small woodland birds were victims.

Qu2. Does removing an aggressive, overabundant bird increase foraging rates for vulnerable species?

We first modelled the sum of foraging events of all species. The dominant species observed foraging, *Pardalotus striatus* (striated pardalote), accounted for 63% of all foraging events by small woodland birds. We therefore repeated models excluding *Pardalotus striatus* to assess the effect of the cull on less common species.

To quantify how foraging rates of different species of small woodland birds responded to the cull of *Manorina melanocephala*, we completed a multivariate analysis, fitting GLMMs by species for species detected foraging four or more times across the period of the study. We used R package Boral as this package is designed for multivariate abundance datasets. It uses Bayesian Markov chain Monte Carlo methods to estimate coefficients of variables and accounts for any correlation between response variables by incorporating possible latent variables due to unmeasured covariates. This allows inference about treatment effects at a community level (Hui 2016). We used a Poisson distribution with log link function, used Farm as a random effect and report model results based on 10 000 iterations of the Bayesian Markov chain Monte Carlo estimation method.

Results

Qu 1. Does removing an aggressive, overabundant bird reduce interference competition for vulnerable species?

Aggressive interspecific interactions are common in this landscape. Across all sites and both phases of our experiment, we observed a total of 253 aggressive interspecific interactions. The average rate of such interactions per hour per 2ha site in the pre-cull phase was 1.19 in control sites and 0.59 in treatment sites. 24 bird species harassed other species and 43 species were victims of harassment, including the 24 aggressor species (Figure 2, Table S3, Table S4). Two of the 43 victim species were mammals, *Antechinus flavipes* (yellow-footed antechinus) and *Vulpes vulpes* (European fox), these two species

suffering a total of four harassment events (Table S3). Across all pre-cull surveys, *Manorina melanocephala* was responsible for 65.7% of harassment events with the next biggest aggressors being *Lichenostomus penicillatus* (white-plumed honeyeater) (7.5%) and *Cracticus tibicen* (Australian magpie) (7.1%) (Table S4). 10 of the 41 avian victim species were small woodland birds (Table S3). We observed a total of 41 harassment events where small woodland birds were victims and a total of 208 events where other birds were victims (Table S3).

We found no evidence of a reduction in the total number of harassment events recorded following the cull, either for models which included all victim species or for models which included only small woodland birds (Figure 3, Table S6). For models which included all victim species, the model with lowest AIC score included the base BACI variables plus Topographic Wetness Index and Corrected Perimeter to Area Ratio for woodland patches. However, five other candidate models had an AIC score within two units of this model (Table S8), the most parsimonious of these being the base BACI model. Similarly, the best model for small woodland birds included only the BACI base variables (Table S8). Table S6 shows coefficient estimates for the best harassment models. We found no evidence of a treatment effect on the amount of harassment by *Manorina melanocephala* (Table S9, Figure S2).

Qu 2. Does removing an aggressive, overabundant bird increase foraging rates for vulnerable species?
We recorded small woodland birds foraging in 180 out of 256 surveys. Across all sites and both phases of our experiment, we observed foraging by 17 species of small woodland bird at an average rate of 4.5 foraging events per hour per 2ha site. *Pardalotus striatus* accounted for 3.0 foraging events per hour of this total. For all species other than *Pardalotus striatus,* we observed foraging in fewer than 13% of surveys in the pre- cull phase.

To explain the differences between foraging rates of small woodland birds in treatment and control sites following the cull, four candidate models which included the BACI base variables (Treatment, Phase and Treatment:Phase interaction) had AIC scores within two units of each other (Table S10). The two most parsimonious of these models each contained six explanatory variables:

Treatment + Phase + Treatment:Phase + Area + Forest extent at 1000ha + Total stems

Treatment + Phase + Treatment:Phase + Area + Total stems + Topographic Wetness Index

For both of these models, foraging rates increased in the post-cull breeding season in treatment sites (Figure 4a) and the relative increase in treatment sites was greater by a factor of two than in control sites (Figure 4b). Coefficient estimates are given in Table S11.

For models excluding *Pardalotus striatus*, six candidate models had AIC scores within two units of each other (Table S12). The two most parsimonious of these were the same as for the models which included

all species, reported above. According to these two models, the relative increase in foraging in treatment sites was a factor of 10 greater than in control sites in the post-cull phase (Figure 5). Table S13 shows coefficient estimates for these two models.

Of the ten species of small woodland bird included in our multivariate analysis, *Lichenostomus penicillatus, Smicrornis brevirostris* (weebill) and *Rhipidura leucophrys* (willie wagtail) showed a significant increase in foraging rate in treatment compared to control sites following the cull (Figure 6). None of the remaining species showed a significant change in foraging rates.

Discussion

We conducted an experimental removal of an overabundant bird, *Manorina melanocephala*, whose extreme interference competition is listed as a Key Threatening Process due to its impact on declining small woodland birds. We monitored the effects on both the culled species (Beggs et al. 2019b) and target species (small woodland birds). Our purpose was to test the resource availability hypothesis of competition in the case of interference competition by monitoring foraging and harassment rates of target species before and after reducing the abundance of the competitively-dominant species. Unexpectedly, we found no evidence of a change in harassment rates following the cull in spite of the decline in *Manorina melanocephala* abundance. Equally unexpectedly, given the consistent harassment rates, we recorded increased foraging rates for some target species. In the remainder of this discussion, we explore the results of our experiment more fully and consider the significance of our findings for competition theory and for management of overabundant or invasive species that exert their effects through interference competition. We also discuss some of the limitations to our study and how these might be overcome in future studies.

Qu 1. Does removing an aggressive, overabundant bird reduce interference competition for vulnerable species?

The competitively-dominant species, *Manorina melanocephala*, was the aggressor in 66% of harassment events in the pre-cull phase. The reduction in *Manorina melanocephala* abundance in treatment sites post-cull was 34% greater than in control sites. We therefore expected a post-cull reduction in the amount of harassment suffered by small woodland birds in treatment sites compared to control sites of approximately 66% x 34% = 22%. Unexpectedly, we found no evidence of a reduction in harassment of small woodland birds Indeed, the direction of the effect suggested a relative increase in harassment in treatment sites post-cull (Figure 3). Neither was there evidence of a reduction in harassment of all victim species as a result of the cull (Table S9). Due to the extreme collective aggression of *Manorina*

melanocephala at even low densities, it is possible that the modest reduction in abundance achieved as a result of the cull was insufficient to show any detectable effect on harassment rates. We also considered the possibility that other aggressive species compensated for the decline in harassment due to reduced abundance of *Manorina melanocephala*. Because of the role of *Manorina melanocephala* in structuring species assemblages (Maron et al. 2013), we term this "social release", analogous to hypotheses such as mesopredator release (Crooks et al. 1999) or competitive release (Kunte 2008). Such an effect has been seen in artificial nest predation studies, for example (Robertson et al. 2014). Compensatory processes are common in management actions that involve removal of overabundant or invasive species (Carter et al. 2007, Choquenot 1991, Marlow et al. 2015). This makes monitoring of outcomes for target species even more important, particularly in cases where compensation involves negative consequences for target species due to unexpected interactions with other species (Norbury et al. 2013, Oppel et al. 2014, Smith et al. 2017) or other disturbances (Doherty et al. 2015). However, due to the low detection rates of harassment and foraging of small woodland birds in this study, we are unable to draw firm conclusions about any social release effect or compensatory responses by other aggressive bird species.

Qu 2. Does removing an aggressive, overabundant bird increase foraging rates for vulnerable species?
In spite of the failure of the cull to reduce harassment rates, there was a two-fold increase in foraging rates for target species in treatment compared to control sites following the cull (Figure 4). This effect was ten-fold when we excluded from models the species most commonly observed foraging (Figure 5). The increase in foraging was species-specific, most small woodland bird species detected recording no change in foraging rates (Figure 6). Three species benefitted from the cull by a relative increase in foraging in treatment sites compared to control sites by a factor of between 7.4 and 54.6 (Figure 6). In the case of these three species, this may be a confirmation of the resource availability hypothesis as an explanation of the impact of *Manorina melanocephala* on small birds (Mac Nally et al. 2005, Maron et al. 2013). However, these three species (*Lichenostomus penicillatus, Smicrornis brevirostris* and *Rhipidura leucophrys*) were among the commonest small woodland birds observed foraging in study sites and appeared better able to coexist with *Manorina melanocephala* than other less common species. Indeed, *Lichenostomus penicillatus* and *Rhipidura leucophrys* are themselves aggressive species and accounted for 7.5% and 3.6% respectively of total harassment events in this study (Table S4). They were also the only small woodland birds observed to harass *Manorina melanocephala* (Figure 2).

Interspecific interactions, the distribution of species and unexpected outcomes in field experiments

The counterintuitive combination of increased foraging rates and consistent harassment rates is not easy to explain. According to the resource availability hypothesis of interspecific competition, we would expect these variables to change in inverse proportion to each other. Our study appears to confirm that resource availability, and by extension species co-occurrence, is not solely determined by competition. Whilst distribution of species is influenced by interspecific interactions, a range of other factors also influence it. Many studies have used the geographic distribution of species to infer the effect of interspecific interactions on species assemblages (Connor et al. 2013, Mac Nally et al. 2012, Mönkkönen et al. 2017). Clear causality is hard to prove through co-occurrence networks, however, since interspecific interactions are not the only determinant of species distribution; environmental factors are also significant (Houlahan et al. 2007, Mutshinda et al. 2009, Ricklefs 2013). With respect to competition, co-occurrence studies are also limited in their ability to distinguish the individual effects of a range of interspecific associations such as positive, facilitative and non-trophic interactions (Bertness et al. 1994, Bruno et al. 2003, Cardinale et al. 2002). Field experiments can more clearly indicate causality and the nature of interactions (Connell 1983, Goldberg et al. 1992, Gurevitch et al. 2000, Schoener 1983) but are often practically limited in scale so the two methods are useful complements. In our case study, in spite of a well-designed experimental approach, a clear causal relationship between competition and resource availability proved difficult to show: the effects of the removal of the key competitive species were limited by an inability to reduce abundance to ecologically significant levels. Despite twice removing *Manorina melanocephala* completely from treatment patches (a total of 538 birds at a cost of AU$13069), compensatory immigration occurred almost immediately (Beggs et al. 2019b). Similar compensatory immigration has been reported in other culls of *Manorina melanocephala* (Davitt et al., 2018, Grey et al., 1998) and other taxa (Grarock et al., 2012, Kierepka et al., 2017, King et al., 2011, Lazenby et al., 2015). Given the extreme effect of even low densities of *Manorina melanocephala* on species assemblages, the modest reduction in abundance of *Manorina melanocephala* achieved by our cull may mean little detectable impact on levels of harassment.

The effects of our failure to achieve substantial reductions in *Manorina melanocephala* abundance were compounded by our small sample size (eight replicates). Site selection in this agricultural landscape was constrained by the need for high detection rates of *Manorina melanocephala*, similar vegetation characteristics and a landholder willing to host the study. Combined with the low detection rates of small birds in sites, this meant that the study had low statistical power. Our study is a reminder that the best experimental designs can fail to show what was intended due to unforeseen outcomes.

It is possible that, had we invested in continued culling, we would have achieved more substantial reductions in *Manorina melanocephala* abundance and therefore seen a greater effect on foraging and harassment rates. The study, however, had a clear aim in assessing the effectiveness of culling as a management tool practically applicable at the enormous scale over which *Manorina melanocephala* exerts its effects. We considered, therefore, that such expense would be prohibitive in any practical management situation. It may be that in less modified vegetation configurations, culling could be effective (see (Crates et al. 2018)), but it is essential to know this before committing conservation resources to culling at a broader scale.

A positive outcome of the recolonisation we observed is that it highlights the lack of knowledge of the basic ecology of *Manorina melanocephala* in the novel ecosystems of this highly modified agricultural region. We do not know from where recolonising birds came or what drivers encouraged their dispersal. Such information is essential if we are to discover a successful culling configuration. We have retained the bodies of all culled birds from this study for future genetic studies which could indicate relationships between the metapopulations in the two waves of recolonisation. Future banding studies could also aid in determining the origins of recolonising birds and the distances over which they are prepared to disperse to occupy vacated territory.

A further limitation of our study was a possible inherent difference between treatment and control sites. We chose treatment/control replicates with comparable vegetation characteristics and found no inherent differences between treatment and control sites in response of *Manorina melanocephala* abundance to the cull (Beggs et al. 2019b), in artificial nest predation rates (Beggs et al. 2019a), nor in foraging rates in this study. However, we recorded a large difference in pre-cull harassment rates between treatment and control sites (Figure 3; Figure S5). Whether this represents a real difference between treatment and control sites or is simply a random result of the small sample size of harassment events where small woodland birds were victim (N = 41), is difficult to say.

Possible explanations for our counter-intuitive findings
Annual rainfall, the chief determinant of productivity in this region of irregular rainfall, was 59% higher in the post-cull year than in the pre-cull year (Bureau of Meteorology, 2017) (Figure S1). Hence, there may have been greater avian activity generally in the post-cull phase due to an increase in resource availability. This might explain the modelled 39% increase in foraging in the post-cull season in treatment and control sites combined (Figure 4, Table S11 - Phase). More small woodland birds foraging in sites might then also provide more targets of harassment.

We also considered changes in the proportion of harassment by *Manorina melanocephala* as a possible explanation. While there was no difference in the total amount of harassment conducted by *Manorina melanocephala* against all victim species in the pre-cull and post-cull phases (Figure S2, Table S9), there was a decline in the proportion of total harassment conducted by *Manorina melanocephala* in treatment sites (Figure S3). There is a general belief that harassment by *Manorina melanocephala* is of greater intensity than harassment by other species because *Manorina melanocephala* defends territory co-operatively and is perceived to be more persistent in its attacks. Hence, the decline in proportion of harassment by *Manorina melanocephala* could indicate an overall decline in intensity of harassment in treatment sites post-cull. Such a decline in harassment intensity, even without a change in harassment rate, could explain increased foraging. However, when we considered harassment of small woodland birds only (rather than all victim species), there was no change in proportion of harassment by *Manorina melanocephala* in treatment sites (Figures S4, S5). However, the low detection rates of harassment events of small woodland birds, particularly in treatment sites (Figure 3; Figures S4, S5), mean it is difficult to make firm conclusions about the relationship between foraging rates and harassment rates.

Interestingly, we found that harassment by *Manorina melanocephala* had neither the biggest mean group size (Figure S6), nor the greatest duration (Figure S7), nor the greatest intensity (which we defined as the product of harassing group size and duration of attack) (Figure S8). GLMMs of harassing group size, duration of attack and harassment intensity showed no treatment effect (Tables S14, S15, S16).

Conclusions

Improvements in opportunities for foraging and reproduction are essential if vulnerable species are to recover in the longer term. Hence, for this experiment we monitored changes in foraging opportunities (reported here) and reproductive potential (Beggs et al. 2019a). In addition, we monitored changes in harassment rates to see if interference competition by the dominant aggressor, or other aggressive species associated with high *Manorina melanocephala* densities, is the reason that small woodland birds are unable to access resources in sites colonised by *Manorina melanocephala*. We showed that even modest reductions in abundance of the dominant aggressor resulted in greater resource availability for some small woodland birds for up to six months. We were unable to show that this was due to less interference competition so our attempt to link the impact of interference competition to resource availability was not wholly successful.

Manorina melanocephala has a preference for small, degraded woodland remnants in fragmented landscapes (Maron et al. 2013, Oldland et al. 2009). Such habitat may have a limited capacity to support recovery of target species (Bennett et al. 2015, Cunningham et al. 2014, Ford 2011, Ikin et al. 2014), even

if the threat from *Manorina melanocephala* is mitigated. Well-designed ecological restoration, particularly where a shrub layer is included, is believed to both deter *Manorina melanocephala* and support declining small woodland birds (Clarke et al. 2010, Hastings et al. 2006, Lindenmayer et al. 2018, Tulloch et al. 2016b). Managing resource supply through ecological restoration may therefore be a suitable complementary policy to managing resource demand through culling of interference competitors.

Declarations

References

Arnold, K. 2000. Strategies of the cooperatively breeding noisy miner to reduce nest predation. - Emu 100: 280-285.

Barrett, G. et al. 2007. Comparison of atlas data to determine the conservation status of bird species in New South Wales, with an emphasis on woodland-dependent species. - Australian Zoologist 34: 37-77.

Barton, K. 2018. MuMIn: Multi-model inference. R package version 1.40.4. - CRAN.

Bechet, A. et al. 2004. The effects of disturbance on behaviour, habitat use and energy of spring staging snow geese. - Journal of applied ecology 41: 689-700.

Beggs, R. et al. 2019a. An experimental test of a compensatory nest predation model following lethal control of an overabundant native species. - Biological Conservation 231: 122-132.

Beggs, R. et al. 2019b. Patch-scale culls of an overabundant bird defeated by immediate recolonisation. - Ecological Applications.

Bennett, J. M. et al. 2015. Fragmentation, vegetation change and irruptive competitors affect recruitment of woodland birds. - Ecography 38: 163-171.

Bertness, M. D. and Callaway, R. 1994. Positive interactions in communities. - Trends in ecology & evolution 9: 191-193.

Brian, M. 1956. Exploitation and interference in interspecies competition. - The Journal of Animal Ecology: 339-347.

Brooks, M. E. et al. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. - The R journal 9: 378-400.

Bruno, J. F. et al. 2003. Inclusion of facilitation into ecological theory. - Trends in Ecology & Evolution 18: 119-125.

Burnham, K. P. and Anderson, D. R. 2003. Model selection and multimodel inference: a practical information-theoretic approach. - Springer Science & Business Media.

Cardinale, B. J. et al. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. - Nature 415: 426.

Carter, S. P. et al. 2007. Culling-induced social perturbation in Eurasian badgers *(Meles meles)* and the management of TB in cattle: an analysis of a critical problem in applied ecology. - Proceedings of the Royal Society B: Biological Sciences 274: 2769-2777.

Case, T. J. and Gilpin, M. E. 1974. Interference Competition and Niche Theory. - Proceedings of the National Academy of Sciences 71: 3073-3077.

Chase, J. M. et al. 2002. The interaction between predation and competition: a review and synthesis. - Ecology letters 5: 302-315.

Choquenot, D. 1991. Density-Dependent Growth, Body Condition, and Demography in Feral Donkeys: Testing the Food Hypothesis. - Ecology 72: 805-813.

Clarke, M. and Fitzgerald, G. 1994. Spatial-Organization of the Cooperatively Breeding Bell Miner Manorina melanophrys. - Emu 94: 96-105.

Clarke, M. F. and Grey, M. J. 2010. Managing an overabundant native bird: the Noisy Miner (Manorina melanocephala). - In: Lindenmayer, D., et al. (eds.), Temperate Woodland Conservation and Management. CSIRO Publishing, pp. 115-126.

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. - The American Naturalist 122: 661-696.

Connor, E. F. et al. 2013. The checkered history of checkerboard distributions. - Ecology 94: 2403-2414.

Crates, R. et al. 2018. Spatially and temporally targeted suppression of despotic noisy miners has conservation benefits for highly mobile and threatened woodland birds. - Biological Conservation 227: 343-351.

Crooks, K. R. and Soulé, M. E. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. - Nature 400: 563.

Cunningham, R. B. et al. 2008. The combined effects of remnant vegetation and tree planting on farmland birds. - Conservation Biology 22: 742-752.

Cunningham, R. B. et al. 2014. The law of diminishing returns: woodland birds respond to native vegetation cover at multiple spatial scales and over time. - Diversity and Distributions 20: 59-71.

Darwin, C. 1859. On the origin of species. - Routledge.

Davitt, G. et al. 2018. Short-term response of a declining woodland bird assemblage to the removal of a despotic competitor. - Ecology and Evolution 8: 4771-4780.

Department of the Environment. 2014. Listing advice - Aggressive exclusion of birds from potential woodland and forest habitat by over-abundant noisy miners -Department of the Environment.

Diller, L. V. et al. 2016. Demographic response of northern spotted owls to barred owl removal. - The Journal of Wildlife Management 80: 691-707.

Doherty, T. S. et al. 2015. Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. - Biological Conservation 190: 60-68.

Doherty, T. S. and Driscoll, D. A. 2018. Competition in the Historical Niche: A Response to Scheele et al. - Trends in ecology & evolution 33: 147-148.

Dow, D. D. 1970. Communal behaviour of nesting Noisy Miners. - Emu 70: 131-134.

Elton, C. S. 1927. Animal ecology. - University of Chicago Press.

Evans, M. C. 2016. Deforestation in Australia: drivers, trends and policy responses. - Pacific Conservation Biology 22: 130-150.

Field, S. A. et al. 2002. Estimating bird species richness: How should repeat surveys be organized in time? - Austral Ecology 27: 624-629.

Ford, H. A. 1979. Interspecific competition in Australian honeyeaters—depletion of common resources. - Australian journal of ecology 4: 145-164.

Ford, H. A. 2011. The causes of decline of birds of eucalypt woodlands: advances in our knowledge over the last 10 years. - Emu 111: 1-9.

Fulton, G. R. 2008. A possible territorial and nesting association between pied and grey butcherbirds Cracticus nigrogularis and C. torquatus and the yellow-throated miner Manorina flavigula. - Corella 32: 30-34.

Goldberg, D. E. and Barton, A. M. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. - The American Naturalist 139: 771-801.

Grarock, K. et al. 2012. Is it benign or is it a pariah? Empirical evidence for the impact of the Common Myna (Acridotheres tristis) on Australian birds. - PLoS One 7: e40622.

Grarock, K. et al. 2014. Understanding basic species population dynamics for effective control: a case study on community-led culling of the common myna (Acridotheres tristis). - Biological invasions 16: 1427-1440.

Grey, M. J. et al. 1997. Initial Changes in the Avian Communities of Remnant Eucalypt Woodlands following a Reduction in the Abundance of Noisy Miners. - Wildlife Research 24: 631-648.

Grey, M. J. et al. 1998. Influence of the Noisy Miner Manorina melanocephala on avian diversity and abundance in remnant Grey Box woodland. - Pacific Conservation Biology 4: 55.

Gu, Z. et al. 2014. circlize implements and enhances circular visualization in R. - Bioinformatics 30: 2811-2812.

Gurevitch, J. et al. 2000. The interaction between competition and predation: a meta-analysis of field experiments. - The American Naturalist 155: 435-453.

Hastings, R. A. and Beattie, A. J. 2006. Stop the bullying in the corridors: can including shrubs make your revegetation more Noisy Miner free? - Ecological Management & Restoration 7: 105-112.

Higgins, P. J. et al. 2001. Handbook of Australian, New Zealand, and Antarctic birds, volume 5: tyrant-flycatchers to chats. - Oxford University Press.

Hinton, J. W. et al. 2013. Red Wolf (Canis rufus) Recovery: A Review with Suggestions for Future Research. - Animals 3: 722.

Hobbs, R. J. and Hopkins, A. 1990. From frontier to fragments: European impact on Australia's vegetation. Proceedings of the Ecological Society of Australia, pp. 93-114.

Houlahan, J. E. et al. 2007. Compensatory dynamics are rare in natural ecological communities. - Proceedings of the National Academy of Sciences 104: 3273-3277.

Hui, F. K. 2016. BORAL–Bayesian ordination and regression analysis of multivariate abundance data in R. - Methods in Ecology and Evolution 7: 744-750.

Ikin, K. et al. 2014. Multi-scale associations between vegetation cover and woodland bird communities across a large agricultural region. - PloS one 9: e97029.

Kierepka, E. M. et al. 2017. Effect of compensatory immigration on the genetic structure of coyotes. - The Journal of Wildlife Management 81: 1394-1407.

King, C. M. et al. 2011. Reinvasion by ship rats (Rattus rattus) of forest fragments after eradication. - Biological Invasions 13: 2391.

Kosciuch, K. L. and Sandercock, B. K. 2008. Cowbird removals unexpectedly increase productivity of a brood parasite and the songbird host. - Ecological Applications 18: 537-548.

Kunte, K. 2008. Competition and species diversity: removal of dominant species increases diversity in Costa Rican butterfly communities. - Oikos 117: 69-76.

Lazenby, B. T. et al. 2015. Effects of low-level culling of feral cats in open populations: a case study from the forests of southern Tasmania. - Wildlife Research 41: 407-420.

Leseberg, N. P. et al. 2014. Fine-scale impacts on avian biodiversity due to a despotic species, the bell miner (Manorina melanophrys). - Austral Ecology.

Lindenmayer, D. 2017. Halting natural resource depletion: Engaging with economic and political power. - The Economic and Labour Relations Review 28: 41-56.

Lindenmayer, D. et al. 2005. Woodlands: a disappearing landscape. - CSIRO PUBLISHING.

Lindenmayer, D. and Cunningham, R. 2011. Longitudinal patterns in bird reporting rates in a threatened ecosystem: is change regionally consistent? - Biological Conservation 144: 430-440.

Lindenmayer, D. B. et al. 2018. Size or quality. What matters in vegetation restoration for bird biodiversity in endangered temperate woodlands? - Austral Ecology 43: 798-806.

Lindenmayer, D. B. et al. 2016. Long-term bird colonization and turnover in restored woodlands. - Biodiversity and Conservation 25: 1587-1603.

Mac Nally, R. 2008. The lag dæmon: hysteresis in rebuilding landscapes and implications for biodiversity futures. - Journal of environmental management 88: 1202-1211.

Mac Nally, R. et al. 2000. Forecasting the impacts of habitat fragmentation. Evaluation of species-specific predictions of the impact of habitat fragmentation on birds in the box–ironbark forests of central Victoria, Australia. - Biological Conservation 95: 7-29.

Mac Nally, R. et al. 2012. Despotic, high-impact species and the subcontinental scale control of avian assemblage structure. - Ecology 93: 668-678.

Mac Nally, R. et al. 2005. Resource availability controls bird-assemblage composition through interspecific aggression. - The Auk 122: 1097-1111.

Marlow, N. J. et al. 2015. Cats (Felis catus) are more abundant and are the dominant predator of woylies (Bettongia penicillata) after sustained fox (Vulpes vulpes) control. - Australian Journal of Zoology 63: 18-27.

Maron, M. et al. 2013. Avifaunal disarray due to a single despotic species. - Diversity and Distributions 19: 1468-1479.

Mönkkönen, M. et al. 2017. Linking species interactions with phylogenetic and functional distance in European bird assemblages at broad spatial scales. - Global ecology and biogeography 26: 952-962.

Moore, A. A. et al. 2016. Green Herons (Butorides virescens) in an Urbanized Landscape: Does Recreational Disturbance Affect Foraging Behavior? - The American Midland Naturalist 176: 222-233.

Mortelliti, A. et al. 2016. Surviving with a resident despot: do revegetated patches act as refuges from the effects of the noisy miner (Manorina melanocephala) in a highly fragmented landscape? - Diversity and Distributions 22: 770-782.

Mortelliti, A. and Lindenmayer, D. B. 2015. Effects of landscape transformation on bird colonization and extinction patterns in a large-scale, long-term natural experiment. - Conservation Biology: n/a-n/a.

Mutshinda, C. M. et al. 2009. What drives community dynamics? - Proceedings of the Royal Society B: Biological Sciences 276: 2923-2929.

Norbury, G. et al. 2013. Invasive mammals and habitat modification interact to generate unforeseen outcomes for indigenous fauna. - Ecological Applications 23: 1707-1721.

O'Connor, R. J. and Hicks, R. K. 1980. The influence of weather conditions on the detection of birds during Common Birds Census fieldwork. - Bird Study 27: 137-151.

OEH. 2015. South Western Slopes - bioregional-scale conservation.

Oldland, J. M. et al. 2009. Habitat preferences of the noisy miner (Manorina melanocephala)–a propensity for prime real estate? - Austral Ecology 34: 306-316.

Oppel, S. et al. 2014. Habitat-specific effectiveness of feral cat control for the conservation of an endemic ground-nesting bird species. - Journal of Applied Ecology 51: 1246-1254.

R Core Team. 2017. R: A language and environment for statistical computing. - R Foundation for Statistical Computing.

Ricklefs, R. E. 2013. Habitat-independent spatial structure in populations of some forest birds in eastern N orth A merica. - Journal of Animal Ecology 82: 145-154.

Robertson, O. et al. 2014. An ecological paradox: More woodland predators and less artificial nest predation in landscapes colonized by noisy miners. - Austral Ecology 39: 255-266.

Robertson, O. J. et al. 2013. Influence of interspecific competition and landscape structure on spatial homogenization of avian assemblages. - PloS one 8: e65299.

Rooney, T. P. et al. 2007. Biotic homogenization and conservation prioritization. - Biological Conservation 134: 447-450.

Schoener, T. W. 1983. Field experiments on interspecific competition. - The american naturalist 122: 240-285.

Smith, H. M. et al. 2017. Exotic black rats increase invertebrate Ordinal richness in urban habitat remnants. - Biological invasions 19: 1315-1328.

Stewart-Oaten, A. et al. 1986. Environmental impact assessment:" Pseudoreplication" in time? - Ecology 67: 929-940.

Suding, K. N. et al. 2004. Alternative states and positive feedbacks in restoration ecology. - Trends in ecology & evolution 19: 46-53.

Thomson, J. R. et al. 2015. Avifaunal disarray: quantifying models of the occurrence and ecological effects of a despotic bird species. - Diversity and Distributions 21: 451-464.

Tulloch, A. I. et al. 2016a. Dynamic species co-occurrence networks require dynamic biodiversity surrogates. - Ecography 39: 1185-1196.

Tulloch, A. I. et al. 2016b. Using empirical models of species colonization under multiple threatening processes to identify complementary threat-mitigation strategies. - Conservation Biology 30: 867-882.

Zuur, A. et al. 2009. Mixed effects models and extensions in ecology with R. Gail M, Krickeberg K, Samet JM, Tsiatis A, Wong W, editors. - New York, NY: Spring Science and Business Media.

Figure Legends

Figure 1. Study region and experimental design. a) Paired treatment/control study patches on study farms. Numbers in boxes refer to farm number. b), c) Maps showing relationship of treatment and control patches, and landscape configuration, on two representative farms. b) is Farm 2; c) is Farm 4.
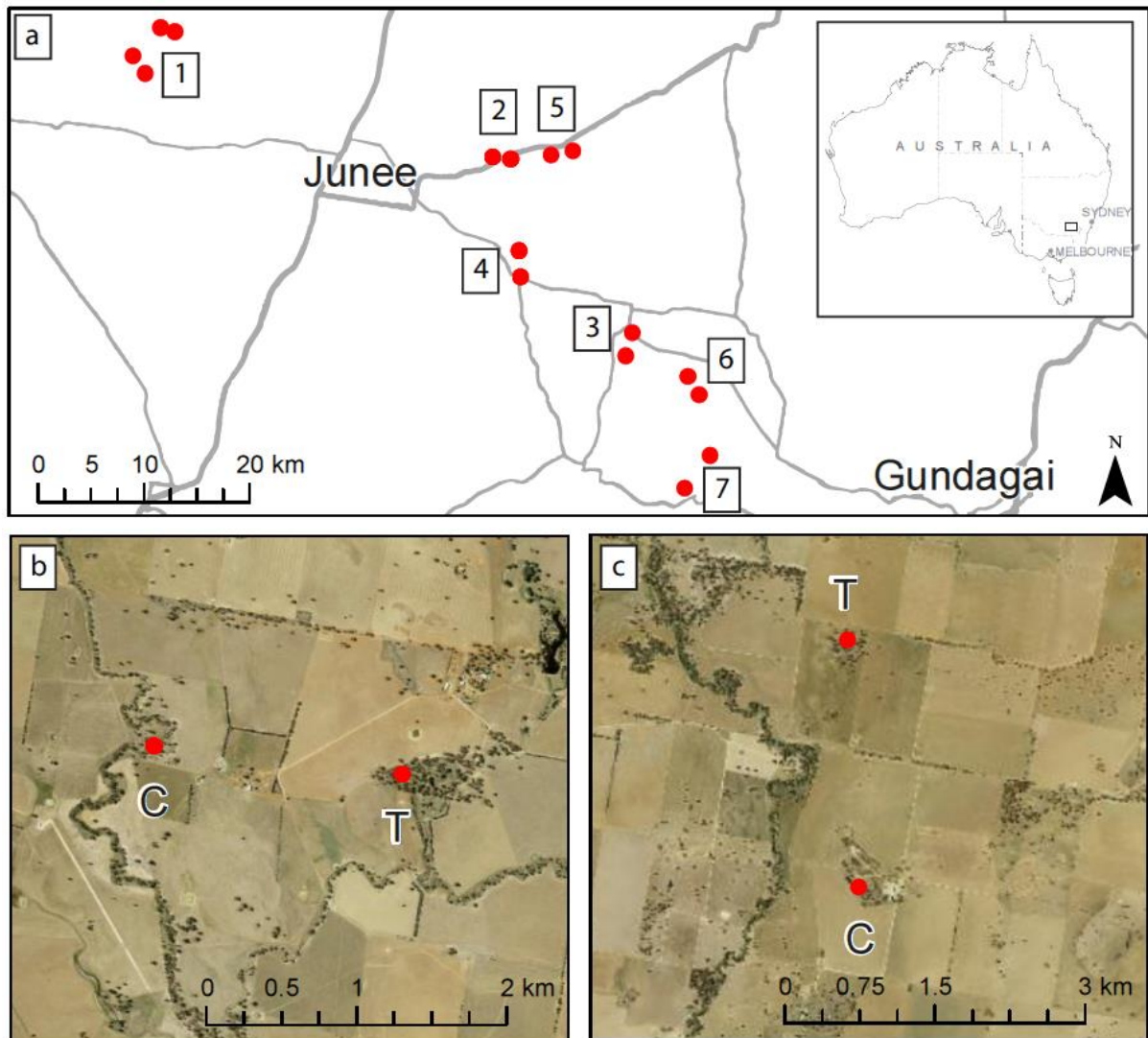
Figure 2. Interspecific harassment networks in study sites before the cull (Treatment and Control sites aggregated). Coloured arcs are labelled with each species that was involved in aggressive interactions either as aggressor, victim or both. Chords of same colour as labelled arc indicate an aggressive interaction perpetrated by the labelled species. Where chords intersect with an arc of different colour, the different coloured arc denotes the victim of aggression. Thickness of chord indicates quantity of interactions. See Table S5 for species glossary.
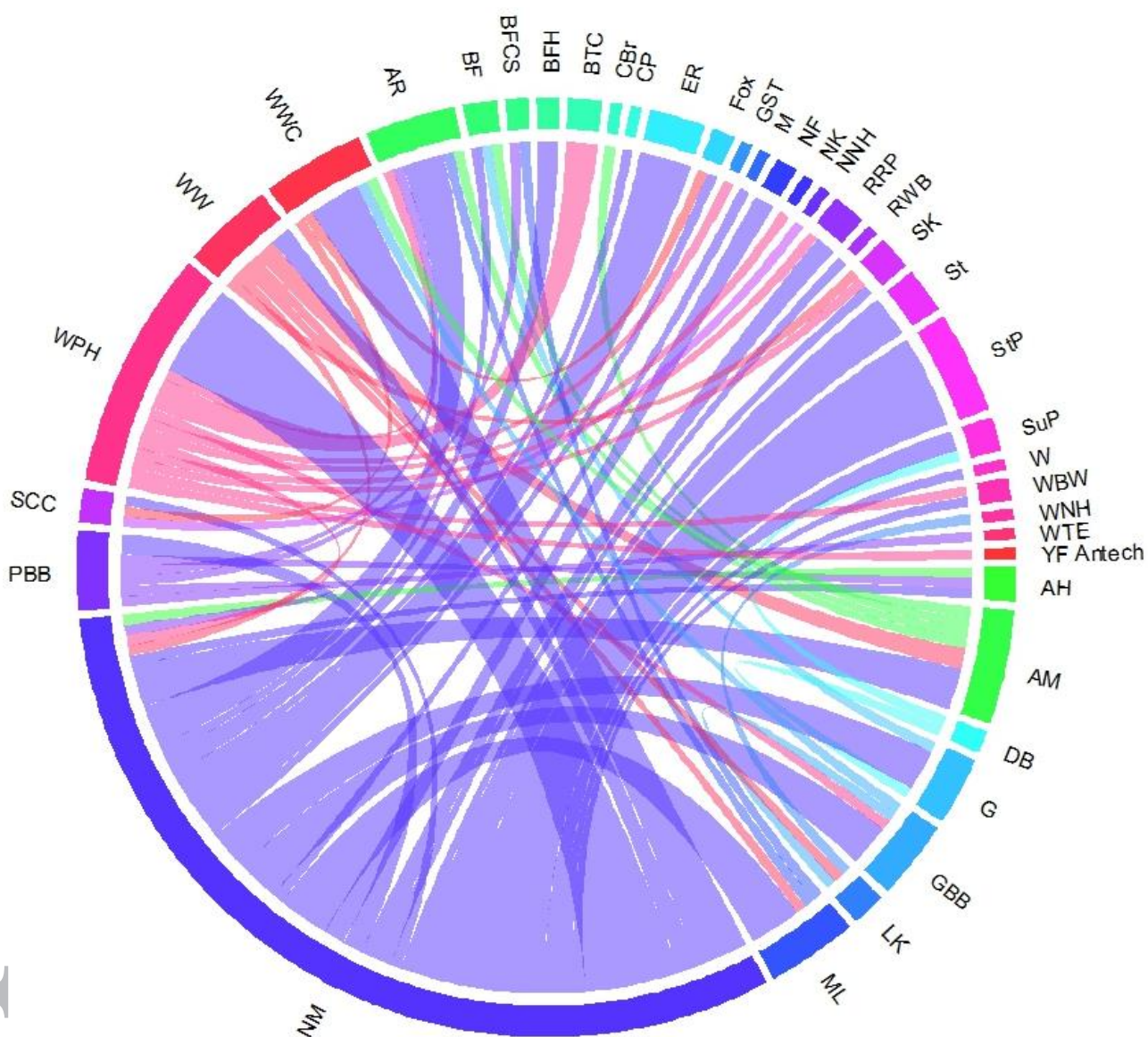
Figure 3. (a) Expected harassment rate of small woodland birds based on the best model, with 95% confidence intervals. Harassment rate is number of harassment events per 2ha site per hour (b) Ratio of expected harassment rates in control and treatment sites before and after the cull. The dotted line at 1.0 represents a ratio of 1 i.e. no difference between the expected harassment rates in the before and after phase. The rightmost plot is the relative difference in the after/before ratio for Treatment and Control. Best model included only BACI base variables: Treatment, Phase and Treatment:Phase interaction.
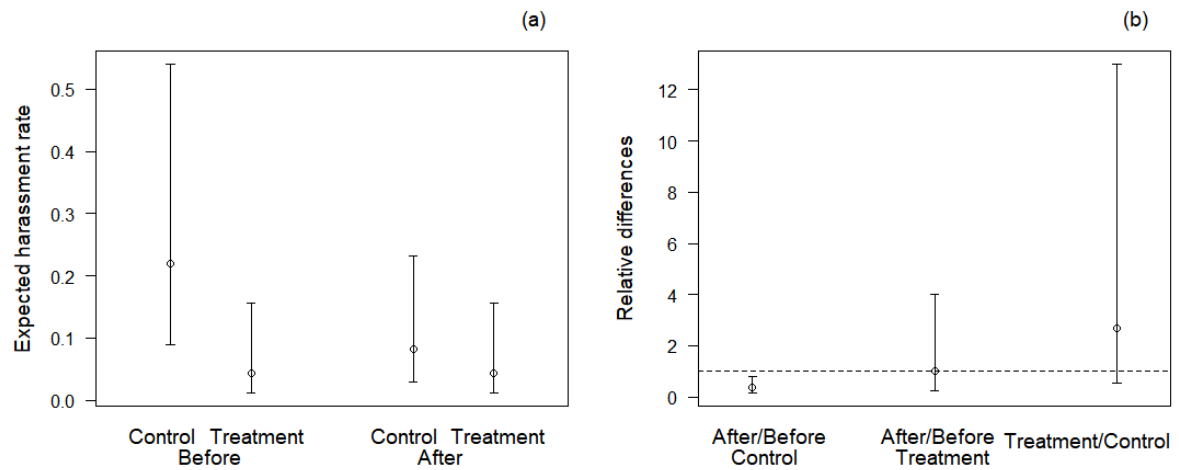
Figure 4. (a) Expected mean hourly foraging rate per 2ha site for small woodland birds based on the best model, with 95% confidence intervals. Foraging rate is number of foraging events per 2ha site per hour (b) Ratio of expected foraging rates in control and treatment sites before and after the cull. The rightmost plot is the relative difference in the after/before ratio for Treatment and Control. Best model included BACI base model + Area + Forest extent at 1000ha + Total stems.
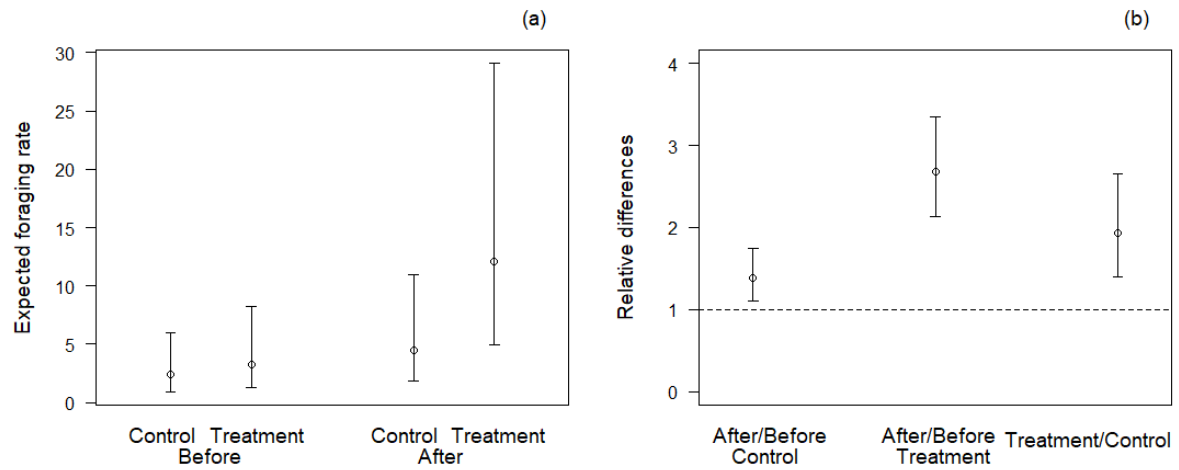
Figure 5. (a) Expected foraging rate of small woodland birds based on the best model excluding *Pardalotus striatus*, with 95% confidence intervals. (b) Ratio of expected foraging rates in control and treatment sites before and after the cull. The rightmost plot is the relative difference in the after/before ratio for Treatment and Control. Best model included BACI base model + Area + Forest extent at 1000ha + Total stems.
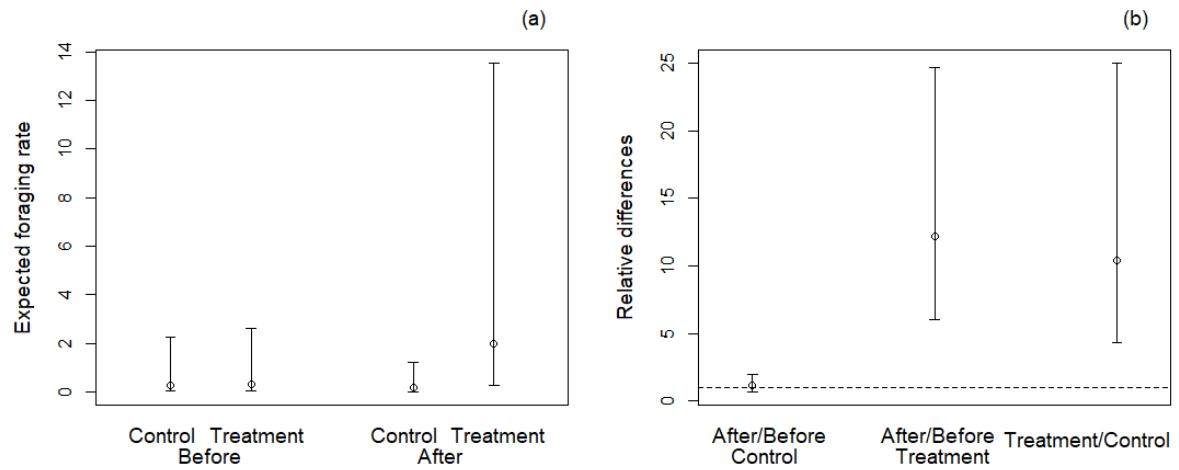
Figure 6. Treatment effect by species. Each plot shows the log of the ratio of the expected relative change in foraging rates in the post-cull compared to pre-cull phase for treatment compared to control sites, with 95% confidence intervals. The dotted line at 0 represents a log ratio of 0 i.e. no difference between treatment and control sites in the post-cull compared to pre-cull phase. Bold lines show species that saw a significant change in the amount of foraging in treatment compared to control sites in the post-cull period.