

A reverse keystone species affects the landscape distribution of woodland avifauna: a case study using the Noisy Miner (*Manorina melanocephala*) and other Australian birds

Rebecca M. Montague-Drake ·
David B. Lindenmayer · Ross B. Cunningham ·
John A. Stein

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Abstract We explored the effects of a purported ‘reverse keystone species’, the Noisy Miner (*Manorina melanocephala*) using a long-term, large-scale dataset. Specifically, we identify whether this aggressive bird affects the landscape distribution patterns of other avifauna, by displacing them into, or restricting their distribution to, less productive areas, and in so doing, adheres to ‘isoleg theory’. We sought to determine the effect of abundance of the Noisy Miner on the abundance of other birds (individual species and groups), and determine whether that effect was consistent with varying site productivity, using a negative binomial distribution with a logarithmic link function, and an offset variable to account for variations in search effort. Relationships between abundance of Noisy Miners and habitat variables were examined using a Poisson distribution with a logarithmic link function scaled for extra-variation (quasi-Poisson regression). We demonstrate that when Noisy Miner abundance is low, many small passerine species are more abundant on high productivity sites.

However, as Noisy Miner abundance increases, small passerine abundance decreases, with this decrease most apparent on productive sites. The same patterns were not evident for birds considered ‘non-competitors’ of the Noisy Miner. We identify that both site productivity and vegetation structure influence the abundance of the Noisy Miner. We reveal that the species increasingly tolerates ‘less desirable’ habitat attributes with increasing site productivity. The preference of the Noisy Miner for productive areas is likely to have deleterious impacts on the long-term survival and reproductive success of other Australian woodland bird species, many of which have already undergone severe declines.

Keywords Reverse keystone species · Isoleg theory · Noisy Miner · *Manorina melanocephala* · Temperate woodlands · Conservation management · Woodland avifauna

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R. M. Montague-Drake (✉) · D. B. Lindenmayer ·
R. B. Cunningham · J. A. Stein
Fenner School of Environment and Society,
The Australian National University, W.K. Hancock
Building, Canberra, ACT 0200, Australia
e-mail: becmd@westnet.com.au

Introduction

An understanding of the factors influencing the distribution and abundance of plants and animals is central to the field of ecology. Competition and aggressive interactions are two such factors and can result in local extinctions (e.g. Bengtsson 1989), reduced fecundity (e.g. Bach et al. 1976), altered habitat use (e.g. Mac Nally and Timewell 2005) and changed behaviour (e.g. Dejean et al. 2005) in a

subordinate species. The effects of aggressive interactions among taxa may be most marked where a particular species has recently been introduced to an area from which it was previously absent (e.g. Wootton 1987) or a given species has undergone significantly increased demographic success as a result of anthropogenic landscape change (see Dow 1977; Garrett et al. 1993).

An example of a species benefiting from landscape change is the Noisy Miner (*Manorina melanocephala*). The Noisy Miner is a large honeyeater (Meliphagidae) that has increased in abundance and distribution since European settlement in south-eastern Australia (Barrett et al. 2007). It is sedentary, lives in communal groups and establishes well-defined territories from which it displaces other species (Dow 1977). Piper and Catterall (2003) suggested that the Noisy Miner may be a ‘reverse keystone species’. That is, where it occurs in moderate to high abundance, the composition of the bird community is significantly altered. Several studies have shown that the diversity and abundance of avifauna is significantly reduced in remnants of native vegetation where this species is present compared to similar remnants from which it is absent (Piper and Catterall 2003; Clarke and Oldland 2007; Maron 2007; Maron and Kennedy 2007; Kath et al. 2009). Such differences appear to be direct results of aggression by the Noisy Miner (and not mediated by habitat) (see Grey et al. 1997).

The preferred habitat of the Noisy Miner includes patches of remnant native vegetation with a high edge: interior ratio (Piper and Catterall 2003; Taylor et al. 2008) and a low density of stems with limited understorey and/or midstorey cover (Maron 2007; Maron and Kennedy 2007; Kath et al. 2009; Lindenmayer et al. 2010). However, these kinds of vegetation attributes are typically found in the most productive parts of a landscape, where agriculture is usually conducted most intensively thereby leading to simplification of vegetation structure. Indeed, recent work by Taylor et al. (2008) and Oldland et al. (2009) suggested that productivity was the primary driver of patch occupancy by the Noisy Miner. If Noisy Miner habitat suitability is determined by productivity, not vegetation structure, recent recommendations to control Noisy Miner dominance via dense planting of understorey species, such as *Acacia* spp. (e.g. Lindenmayer et al. 2010) or reducing the edge: interior ratio of vegetation patches through the planting of

buffers (e.g. Taylor et al. 2008) may be ill-founded. Whether Noisy Miner habitat suitability is determined by productivity or vegetation structure also has implications for other avifauna. For instance, ‘isoleg theory’ describes how the increasing density of a behaviourally dominant species in superior habitats will reduce the numbers of subordinate species, which then must congregate in poorer habitats (see Mac Nally and Timewell 2005). Ford (1979) similarly theorised a dominance hierarchy for Australian honeyeaters in which the largest species aggressively defend the best nectar resources with smaller honeyeaters either adopting special behaviours (inconspicuousness or flocking) to obtain access to better flowering sites or using poorer flowering areas. Thus, if the Noisy Miner does select sites based on productivity this ‘reverse keystone species’ may affect the landscape distribution patterns of other woodland avifauna, particularly small honeyeaters and other insectivorous birds, by displacing them into, or restricting their distribution to, less productive parts of the landscape with negative impacts on their survival and reproductive success.

Using a dataset collected at 138 sites between 2001 and 2008, we addressed key knowledge gaps regarding the factors affecting the distribution and abundance of the Noisy Miner and a suite of other birds in the temperate woodlands in southern New South Wales, south-eastern Australia. Specifically, we aimed to:

1. Determine whether productivity and/or vegetation structural attributes were the main drivers of Noisy Miner abundance within woodland remnants. At the onset of our investigation, we predicted that *both* vegetation structure and site productivity would have a strong effect on abundance of the Noisy Miner occupying woodland remnants.
2. Determine whether this ‘reverse keystone species’ adheres to ‘isoleg theory’ (and the dominance hierarchy proposed by Ford 1979) and thus affects the distribution patterns of other avifauna, in particular, potential competitors (i.e. small birds with a high dietary level of overlap with the Noisy Miner), by displacing them into, or restricting their distribution to, less productive areas. We predicted that when the abundance of the Noisy Miner was low, perceived competitors would be

most abundant on high productivity sites. Conversely, when the Noisy Miner was abundant, potential competitors would be more abundant on low productivity sites. This would not be the case for ‘non-competitor’ species and so there would be no evidence of any Noisy Miner abundance by site productivity interactions. These assertions, shown schematically in Fig. 1, are consistent with ‘isoleg theory’.

Methods

Study region

We conducted our study in the South West Slopes (SWS) region of New South Wales which is part of Australia’s eastern ‘wheat-sheep belt’. Approximately 85% of the original cover of native vegetation in the SWS has been removed in the past 200 years, primarily for agriculture (Lindenmayer et al. 2005).

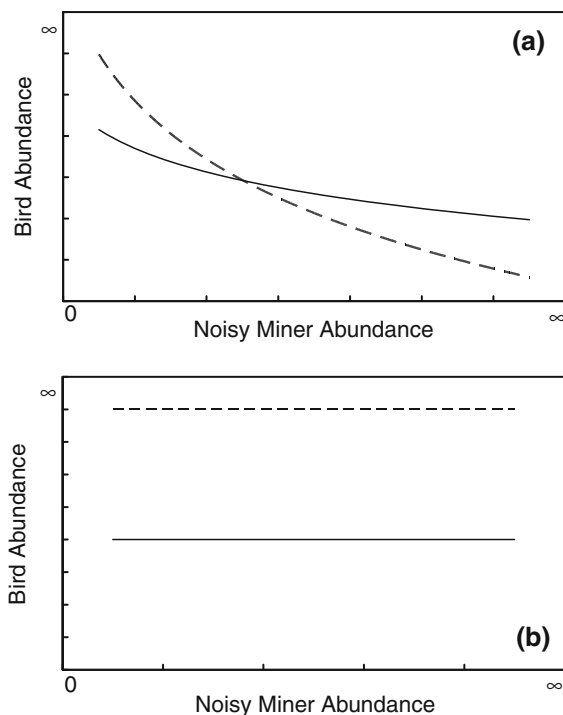


Fig. 1 Schematic representation of a plausible model for the joint effects of Noisy Miner abundance and productivity on bird abundance for **a** ‘perceived-competitors’ and **b** ‘non-competitors’. The solid line indicates lower productivity sites. The dashed line indicates sites of higher productivity

The predominant form of native vegetation in the region is temperate woodland. Most remaining temperate woodland remnants are small (<10 ha) and are suffering habitat degradation through inappropriate grazing and burning regimes, invasion of exotic grasses and weeds, rising saline groundwater levels, and eucalypt dieback caused by inappropriate fertilizer application and insect attack (Lindenmayer et al. 2005).

Study sites

Our study comprised 138 temperate woodland remnants located on 46 farms on the SWS. Remnant size, condition and context were highly variable (see electronic supplementary material 1). We located our sites and farms in an area between the towns of Junee (0552952E 6140128N) in the north, Albury (0494981E 6008873N) in the south, and Gundagai (600532E 6119073N) and Howlong (467090E 6017897N) in the east and west respectively. Site vegetation belonged to one of four ‘Keith Classes’ (see Keith 2004). These included ‘Floodplain Transition Woodlands’, primarily dominated by grey box (*Eucalyptus microcarpa*) and yellow box (*E. melliodora*) and to a lesser extent, white cypress pine (*Callitris glaucophylla*), ‘Inland Riverine Forests’, primarily dominated by river red gum (*E. camaldulensis*), ‘Upper Riverina Dry Sclerophyll Forests’, primarily dominated by white box (*E. albens*), Blakely’s red gum (*E. blakelyi*), mugga ironbark (*E. sideroxylon*), red stringybark (*E. macro-rhyncha*) and red box (*E. polyanthemus*) with occasional white and black cypress pine (*C. endlicheri*), and ‘Western Slopes Grassy Woodlands’, primarily dominated by white box with kurrajong (*Brachychiton populneus*), white cypress pine, Blakely’s red gum and yellow box. The sites spanned a range of structural conditions—old growth, natural seedling regrowth and coppice (i.e. multi-stemmed) regrowth woodland. No sites had native vegetation plantings present. Our field sites have been subject to a range of grazing regimes.

Bird surveys

We established a field site within each of our 138 temperate woodland remnants. Each site consisted of three permanent markers evenly spaced along a 200 m transect. Bird surveys were conducted at each of the three permanent markers at each site using the 5 min

point-interval count method (*sensu* Pyke and Recher 1983). Each survey was completed by two different observers on two different days to minimise observer and weather effects (see Cunningham et al. 1999). We conducted all counts between 0530 and 0930 h. Spring surveys were conducted in early November (which is the peak breeding season in the study region, when most summer migrants are present and birds have established territories and exhibit strong patterns of site fidelity). Winter surveys were conducted from mid-June to early July, when ‘altitudinal migrants’ are present. We recorded the abundance of all birds seen or heard in discrete distance classes at each of the three permanent markers at each site. Birds were excluded if they were greater than 50 m from the observer or overhead to ensure each survey plot was independent. We completed surveys in spring 2002, winter 2004, spring 2004, spring 2006, winter 2007, winter 2008 and spring 2008. We aggregated our data across all years and observers at a site. Effort was standardised across all years (as a few of our field sites had been established slightly longer than others) either by dividing the total abundance of a bird species at a site by the total number of point counts, or by including an offset variable in the statistical model.

Vegetation data and other covariates

We measured site-based covariates as well as other broader-scaled (landscape-level) covariates at each site. We have termed site-based attributes (i.e. those broadly relating to habitat degradation) ‘patch content variables’ and attributes characterising the area around the patch (i.e. those related to habitat fragmentation) ‘landscape context variables’. We collected ‘content variables’ as part of extensive field work, whereas we derived ‘context variables’ by examining the area within a 500 m radius of each site using ‘SPOT5’ satellite imagery. We assigned each site a Keith Class, based on the dominant eucalypts or other overstorey species as outlined in Keith (2004). We further outline the covariates used in this study and the methods used to gather them in electronic supplementary material 1.

Site productivity

We used a topographic wetness index (TWI) as a surrogate for site productivity. The TWI is a useful measure for predicting water distribution and gives a

measure of relative position in a landscape. Calculation of a TWI requires a digital elevation model (DEM) with hydrological integrity. Using the ANUDEM algorithm (<http://fennergchool.anu.edu.au/publications/software/anudem.php>), we generated a DEM of the region at a grid resolution of 20 m. Source data comprised 1:25,000 and 1:50,000 scale contours, streams and point heights. We derived surface flow directions from the DEM to allow the upland area of each grid cell to be calculated, which was divided by cell width adjusted for aspect of inflow direction. We then divided this ‘specific catchment’ by the local slope of a given cell. Low values indicate ridges and upper slopes that are steep with small contributing catchments, while values then increase through lower slopes, valley flats, and drainage lines.

We generated a 500 m buffer around the mid-point of each site and calculated the average value of the TWI within each buffer. We assumed that sites with a higher TWI were more productive (because of potentially higher moisture regimes, and the likelihood of deeper soil profiles and higher nutrient loads). Taylor et al. (2008) similarly assumed that altitude was a surrogate for productivity across a narrow band of altitudinal differences within a local region. We also examined the effect of altitude on the abundance of the Noisy Miner within woodland remnants.

Statistical analysis

All statistical computations were undertaken using GenStat (13th Edition, VSN International, UK).

Noisy Miner habitat model

Relationships between abundance of Noisy Miners and all variables relating to patch content, landscape context and productivity (altitude and TWI) were examined using a Poisson distribution with a logarithmic link function scaled for extra-variation (quasi-Poisson regression). Candidate explanatory variables were included in models separately and jointly. The combination of significant variables ($P < 0.05$) with the lowest AIC score was deemed to be the ‘best’ model. This was achieved using a subset models procedure in GenStat. We also searched for possible interactions between the terms included in the best model of Noisy Miner abundance. The level of

collinearity between covariates was assessed using scatter plots combined with expert knowledge.

Effects of Noisy Miners on the landscape distribution of other avifauna

We sought to determine the effect of abundance of the Noisy Miner on the abundance of individual species and birds in a variety of avifaunal groups, and determine whether that effect was consistent on sites with different values for site productivity (as determined by the TWI). We selected these groups (see electronic supplementary material 2) to include: (1) birds which the Noisy Miner is likely to perceive as competitors and/or actively displace, as well as, (2) taxa of which the Noisy Miner is tolerant and therefore likely to co-occur with. We assumed, based on the work of others such as Piper and Catterall (2003), Parsons et al. (2006) and Maron (2009), that the Noisy Miner would be more likely to displace: (1) birds with a small body size (i.e. smaller than that of the Noisy Miner i.e. <60.3 g), (2) birds with a similar diet, and (3) species with conspicuous foraging behaviour (e.g. flycatchers). The abundance of each avifaunal group or species was modelled using a negative binomial distribution with a logarithmic link function, and an offset variable to account for variations in search effort. The negative binomial distribution was found to be a better model than the quasi-Poisson model for the over-dispersion in these data after applying the usual model diagnostics and assessing the residual mean deviance to assess the goodness of fit. Where site occupancy of the avifaunal group or species was less than 58% (as was the case for the Restless Flycatcher and a suite of species of robins), the abundance, given presence, was modelled; i.e. only those sites where the group or species occurred were included in the analysis. We did this because many sites did not support habitat for such birds. Noisy Miner abundance was fitted in the model on the log scale; (i.e. $\log(\text{number of Noisy Miners} + 1)$).

Results

Noisy Miner abundance

We recorded the Noisy Miner at 126 of the 138 remnant woodland sites. The average annual site abundance of the Noisy Miner varied from zero to 24

individuals across all sites. The average annual abundance of Noisy Miners at a site was 7.05 (± 0.56 standard error) individuals.

Noisy Miner habitat model

We found several patch content, landscape context and site productivity variables to be significantly related to the abundance of the Noisy Miner within a woodland remnant when assessed individually using univariate analysis (see Table 1). Variables included TWI, the amount of mistletoe and dieback in the canopy, canopy height, the total number of stems, the number of paddock trees within a 500 m radius of the site, the amount of fallen timber and the vegetation composition (as determined using the Keith Class) (see Table 1). All variables were significant ($P < 0.05$) in that model with the exception of fallen timber, which while not significant ($P = 0.19$) improved model fit. While we have identified our ‘best’ model, we found four other candidates for ‘best’ model, all having AIC scores differing by <2 (see Burnham and Anderson 2002). The AIC scores and associated variables for all such models are shown in electronic supplementary material 3. All of our final models included mistletoe, dieback, canopy height, number of paddock trees within a 500 m radius, the productivity of the site (as determined using the TWI) and the vegetation composition (as determined using the Keith Class). The total number of stems, the amount of fallen timber, stems with a DBH <15 cm and the amount of overstorey cover were present in four, three, two and one models respectively.

Terms of significance that were not ultimately included in the best model, as selected using AIC, were significantly related ($P \leq 0.05$) to one or several of those that were included. For instance, we found that dieback was significantly correlated with the amount of understorey Acacia, the amount of cleared land within a 500 m radius of a site, the amount of remnant woodland within a 500 m radius of a site, the number of stems <15 cm, the number of strata, and midstorey and overstorey cover. In addition, we found that the latter four variables also were significantly related to total stems and canopy height. Our analyses demonstrated that the value for the TWI and the number of paddock trees within a 500 m radius of a site were significantly related to the amount of cleared land and remnant woodland within a 500 m radius of a site and moss and lichen cover.

Table 1 Habitat and productivity variables significantly related to the abundance of the Noisy Miner within woodland remnants

	Variable ^a	Parameter estimate	Standard error of parameter estimate	P-value
Estimates and P-values are obtained by fitting quasi-Poisson models ^a Italicised variables were retained in the 'best' model as identified using lowest AIC criteria ^b In final model, WSGW and FTW significantly preferred over IRF or URDSF (parameter estimate = 0.49, standard error of parameter estimate = 0.21, $P = 0.02$)	Patch content variables			
	Mosses and Lichens	−0.03	0.015	0.04
	<i>Mistletoe</i>	−0.009	0.003	0.006
	<i>Canopy height</i>	+0.05	0.018	0.007
	<i>Dieback</i>	+0.33	0.076	<0.001
	Stems with dbh <15 cm	−0.02	0.008	0.03
	<i>Total stems</i>	−0.02	0.007	0.02
	Strata count	−0.24	0.097	0.02
	<i>Logs</i>	−0.001	0.0007	0.05
	% Acacia in Understorey	−0.01	0.006	0.08
	MS cover	−0.02	0.010	0.07
	OS cover	+0.01	0.005	0.009
	Keith Class	^b	^b	<0.001
	Landscape context variables			
	Clear 500	+0.01	0.007	0.07
	Rem 500	−0.01	0.007	0.06
	<i>PT 500</i>	−0.96	0.266	<0.001
	Productivity variables			
	TWI Middle	+0.15	0.044	<0.001

Two terms in our 'best' model (i.e. the number of paddock trees within 500 m of a site and the total number of stems at a site) exhibited a significant ($P < 0.05$) interaction with the TWI while the amount of mistletoe at a site also suggested a weak interaction with the TWI ($P = 0.058$) (see electronic supplementary material 4). These interactions indicated that the abundance of the Noisy Miner responded differently to changing values of these various habitat elements relative to the values for site productivity, with the species more rapidly declining in abundance with increasing levels of variables with which it was negatively associated at unproductive, relative to productive, sites (see Fig. 2).

We found that the abundance of the Noisy Miner also varied significantly between vegetation communities (i.e. Keith Classes). The Noisy Miner was significantly more abundant in Western Slopes Grassy Woodlands (WSGW) and Floodplain Transition Woodlands (FTW) than either in Upper Riverina Dry Sclerophyll Forests (URDSF) or Inland Riverine Forests (IRF). Many of the variables associated with Noisy Miner abundance varied significantly between the Keith Classes (see electronic supplementary

material 5), but not always in a direction consistent with Noisy Miner productivity preferences. These differences, together with the maintenance of both structural and productivity variables in each of our 'best' models and the nature of the interaction terms between structural and productivity variables, suggest that vegetation structure, vegetation composition *and* productivity were important determinants of suitable Noisy Miner habitat.

The abundance of avifauna and the interaction of Noisy Miner abundance and site productivity

We used a model (i.e. $\text{Abundance} = \text{TWI} + \text{Noisy Miner abundance} + \text{TWI} \times \text{Noisy Miner abundance}$) to assess the effects of productivity and Noisy Miner abundance and the interaction between these two factors on the abundance of birds in selected groups.

For simplicity, we show (Table 2) predictions at two levels of productivity for two levels of abundance of the Noisy Miner. These levels were −0.46 and 1.69 for productivity and 17 and 177 for the abundance of the Noisy Miner (the lower and upper quartiles, respectively). While results are presented for 'high'

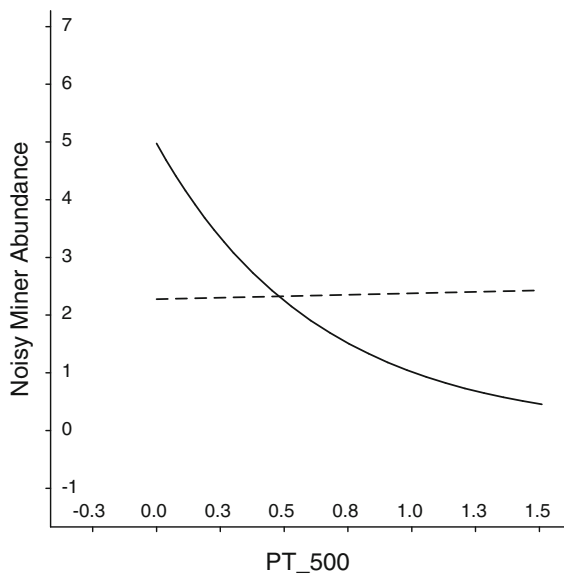


Fig. 2 Interaction between annual Noisy Miner abundance at a site, productivity (*dashed line* indicates more productive sites ($TWI > 0$), *solid line* indicates less productive sites ($TWI < 0$)) and the number of paddock trees within a 500 m radius of the site ($P = 0.002$)

and ‘low’ Noisy Miner abundance, the model underlying the results was based on continuous, not categorical, variables.

Nearly all species/groups of birds showing a negative relationship with the abundance of the Noisy Miner appeared to prefer more productive areas when Noisy Miner abundance was low. When the abundance of the Noisy Miner was high this effect was reversed (see Fig. 3 for an example of such an interaction for ‘small competitors’ using uncategorised data). We did not find this pattern for species positively associated with the abundance of the Noisy Miner.

Discussion

The habitat requirements of the Noisy Miner

One of the primary aims of our study was to quantify the habitat requirements of the Noisy Miner in temperate woodland remnants in southern Australia. In particular, we sought to determine whether site productivity or vegetation structure was the principal determinant of abundance of this species in a woodland remnant. Site productivity obviously has a large

effect on the structure and composition of vegetation at a site, so we gathered a large, long-term data set (138 sites studied over 7 years) to aid the power of our investigations and help disentangle these two closely-related variables. Our results clearly showed that the Noisy Miner responded to both a range of vegetation structural variables *and* site productivity.

Site productivity

We found productivity to be a strong predictor of the abundance of the Noisy Miner within woodland remnants (see Table 1), which is perhaps not surprising because with its year-round territoriality, energy-expensive behaviour and communal lifestyle, the Noisy Miner requires sites with an abundant energy source (Dow 1977). Productivity has previously been found to be an important determinant of animal distribution across a wide range of taxa (e.g. Abramsky and Rosenzweig 1984; Braithwaite et al. 1984, 1989; Currie 1991; Soderquist and Mac Nally 2000). The Noisy Miner’s diet comprises, on average, 25% nectar and 75% insects (Ford 1979). Many canopy-dwelling insects are more abundant on sites with high soil fertility (Recher et al. 1996; Wardell-Johnson et al. 2006). Nectar production also increases with soil moisture (Wilson and Bennett 1999) and tree size (Lindenmayer et al. 2005) and large trees are more abundant on productive sites (Soderquist and Mac Nally 2000). Our results concur with Oldland et al. (2009) and Taylor et al. (2008) in suggesting that productivity is a key driver of Noisy Miner habitat, most likely because such areas offer a more abundant, diverse and temporally-secure food supply.

Vegetation structure

We found that the Noisy Miner was more abundant in sites with a simple vegetation structure in the ground layer (i.e. sites with few logs); the understorey (i.e. minimal understorey Acacia), the midstorey (i.e. little midstorey cover) and overstorey (i.e. sites with abundant dieback and minimal mistletoe) (see Table 1). The Noisy Miner was also negatively associated with high stem densities. Sites that are structurally complex may require the Noisy Miner to expend more energy to detect and dispel perceived competitors, and even then such tactics may not be fully successful (see Dow 1977; Kath et al. 2009; Maron 2009), thereby effectively

Table 2 Predicted means and associated standard errors of the abundance of total birds, cross classified by Noisy Miner abundance and productivity

Bird	Productivity	NM low	NM high	Interaction <i>P</i> -value
Bird abundance decreases with increasing abundance of the Noisy Miner. This decrease is more apparent on productive sites relative to unproductive sites				
Small Honeyeaters	Low	81.01 (±10.11)	28.04 (±4.83)	<0.001
	High	110.60 (±29.79)	11.10 (±1.61)	
Small Competitors	Low	215.7 (±17.43)	89.7 (±9.93)	<0.001
	High	371.7 (±64.69)	67.7 (±6.09)	
Fantails	Low	20.22 (±2.10)	7.24 (±1.06)	<0.001
	High	49.35 (±10.99)	4.31 (±0.54)	
Whistlers	Low	11.14 (±1.58)	3.97 (±0.82)	0.03
	High	12.17 (±3.74)	2.01 (±0.37)	
Woodswallows	Low	34.50 (±6.74)	8.14 (±2.24)	<0.001
	High	150.51 (±63.02)	4.44 (±1.06)	
White-plumed Honeyeater (<i>Lichenostomus penicillatus</i>)	Low	72.56 (±9.00)	26.12 (±4.47)	<0.001
	High	103.58 (±27.71)	10.68 (±1.54)	
Large Honeyeaters ^a	Low	22.17 (±3.59)	25.69 (±5.70)	0.06
	High	13.24 (±4.69)	7.63 (±1.47)	
Restless Flycatcher (<i>Myiagra inquieta</i>) ^a	Low	5.14 (±0.73)	4.38 (±1.14)	0.08
	High	5.88 (±1.83)	2.55 (±0.77)	
Bird abundance decreases with increasing abundance of the Noisy Miner ^b irrespective of site productivity				
Robins	Average	9.64 (±1.06)	7.16 (±1.34)	0.20
Bird abundance increases with increasing abundance of the Noisy Miner ^c and there are more birds on productive compared to unproductive sites ^c				
Large Birds	Low	172.9 (±6.89)	212.6 (±11.85)	0.47
	High	193.8 (±9.41)	238.3 (±9.81)	
Galah (<i>Cacatua roseicapilla</i>)	Low	12.96 (±1.56)	26.11 (±4.26)	0.76
	High	20.66 (±2.97)	41.64 (±5.00)	
Bird abundance increases with increasing abundance of the Noisy Miner ^d irrespective of site productivity				
Eastern Rosella (<i>Platycercus eximius</i>)	Average	19.31 (±1.12)	44.52 (±2.77)	0.94
Granivores	Average	92.6 (±4.22)	134.9 (±6.77)	0.27
Butcherbirds	Average	0.63 (±0.14)	4.43 (±0.55)	0.65
Bird abundance increases with increasing site productivity ^e , irrespective of Noisy Miner abundance				
Laughing Kookaburra (<i>Dacelo novaeguineae</i>)	Low	1.40 (±0.19)		0.63
	High	2.27 (±0.27)		
Pardalotidae	Low	28.15 (±2.93)		0.29
	High	35.89 (±3.58)		
Bird abundance not related to Noisy Miner abundance or site productivity ^f				
Red-rumped Parrot (<i>Psephotus haematonotus</i>)	N/A	N/A	N/A	0.12

Prediction and *P*-values obtained by fitting negative binomial models

^a No significant relationship with Noisy Miner abundance per se, weak evidence for decrease in abundance with increases in the abundance of the Noisy Miner on high productivity sites

^b Robin abundance declines with increasing abundance of Noisy Miners ($P = 0.047$). No relationship between Robin abundance and productivity ($P = 0.45$)

^c The abundance of large birds increases with increasing abundance of Noisy Miners ($P < 0.001$). The number of large birds increases with increasing site productivity ($P = 0.03$). Galah abundance increases with increasing abundance of Noisy Miners ($P < 0.001$). The number of Galahs increases with increasing site productivity ($P = 0.03$)

^d Eastern Rosella abundance increases with increasing abundance of Noisy Miners ($P < 0.001$). No relationship between Eastern Rosella abundance and productivity ($P = 0.68$). Granivore abundance increases with increasing abundance of Noisy Miners ($P < 0.001$). No relationship between Granivore abundance and productivity ($P = 0.16$). Butcherbird abundance increases with increasing abundance of Noisy Miners ($P < 0.001$). No relationship between Butcherbird abundance and productivity ($P = 0.15$)

^e Laughing Kookaburra abundance increases with increasing site productivity ($P = 0.009$). No relationship between Laughing Kookaburra and Noisy Miner abundance ($P = 0.06$). Pardalotidae abundance increases with increasing site productivity ($P = 0.035$). No relationship between Pardalotidae and Noisy Miner abundance ($P = 0.06$)

^f Red-rumped Parrot abundance not related to site productivity ($P = 0.59$) or Noisy Miners ($P = 0.35$)

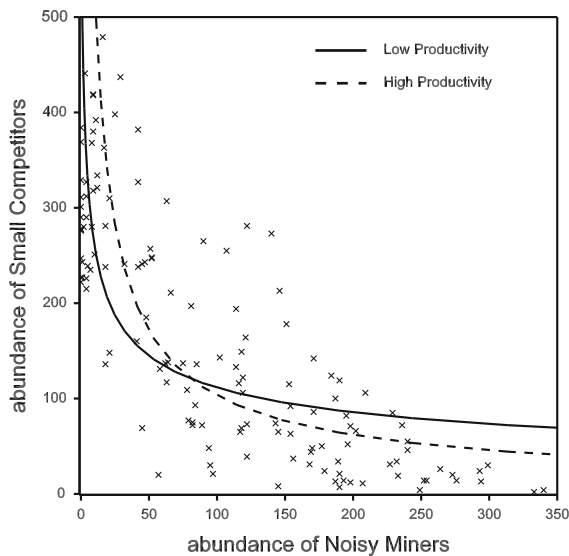


Fig. 3 Plot of the fitted relationship between the abundance of small competitors and the abundance of the Noisy Miner for sites with high (dashed line) and low (solid line) site productivity. Bird abundances are aggregated across all survey periods. Interaction effect significant ($P < 0.001$)

reducing the food supply available for the Noisy Miner. Our results echo previous studies which have found that the Noisy Miner avoids sites with dense understorey or midstorey shrubs, particularly *Acacia* (Hastings and Beattie 2006; Howes and Maron 2009; Lindenmayer et al. 2010), high volumes of coarse woody debris (Maron and Kennedy 2007) and high stem densities (Clarke and Oldland 2007; Maron 2007).

We found that the Noisy Miner was positively associated with dieback and negatively associated with mistletoe (see Table 1). While this may simply indicate that an open canopy allows the Noisy Miner to more easily detect and dispel competitors as outlined above, it also may be because such sites have higher abundances of herbivorous insects (psyllids). Eucalypt tree crowns experiencing increased penetration of sunlight into the canopy (such as when dieback levels are high and mistletoe abundance is low) possess more vigorously developing foliage favourable to psyllids (see Wardell Johnson et al. 2005). Furthermore, epicormic foliage (as found on many eucalypt trees suffering dieback) has higher free amino acid concentrations than mature adult foliage (Wardell Johnson et al. 2005) and thus may also support higher abundances of psyllids. In contrast, Loyn (1987) suggested that the exclusion of small

insectivorous birds by the Noisy Miner causes elevated insect herbivore density, leading to increased dieback. However, Piper and Catterall (2003) found no difference between dieback rates within and outside areas inhabited by colonies of the Noisy Miner. Whether dieback is a result of Noisy Miner occupancy or whether the Noisy Miner preferentially occupies dieback-affected sites is clearly an area requiring further investigation.

Landscape context

We found that the Noisy Miner was related to landscape context, being more abundant at sites surrounded by cleared land, particularly in areas largely devoid of scattered (paddock) trees (see Table 1). Taylor et al. (2008) suggested that the Noisy Miner may better defend patches when the approach of an ‘intruder’ can be readily observed. ‘Intruding’ bird species would be less conspicuous in a ‘soft matrix’ comprised of remnant vegetation and scattered trees. Woodland species may use paddock trees to move between foraging sites (Fischer and Lindenmayer 2002) and are important determinants of site occupancy for many woodland birds (Montague-Drake et al. 2009). Martin et al. (2006) also found that the Noisy Miner was more abundant in sites surrounded by cleared country than woodland. In this study, we also observed a significant interaction between the abundance of the Noisy Miner, site productivity and the number of surrounding paddock trees. This suggests that at sites with a marginal food supply, the cost of defending a patch surrounded by a soft matrix may have been too high to enable occupation by, or build-up of, large groups.

The importance of vegetation structure and productivity

Importantly, our results showed that both productivity and vegetation structure were important determinants of Noisy Miner abundance in woodland remnants. This was demonstrated by:

1. The inclusion of both productivity and vegetation structural variables in the ‘best’ model (and other equally good models) (see Table 1; electronic supplementary material 3);
2. Noisy Miner abundance varied between vegetation communities (i.e. Keith Classes) but not in a

manner consistent with the TWI (see electronic supplementary material 5). For instance, the WSGW sites supported the highest numbers of the Noisy Miner but had the second lowest values for TWI. Conversely, the Noisy Miner occurred least frequently in IRF remnants, which had the second highest TWIs. Major et al. (2001) also found lower Noisy Miner occupancy rates in IRF (*Eucalyptus camaldulensis*) remnants than ‘box gum’ (WSGW) remnants; and

3. Noisy Miner abundance declined more sharply with increasing stems, mistletoe and the number of paddock trees within a 500 m buffer of the remnant at low productivity sites, than at sites of high productivity. These findings suggest that the Noisy Miner can better tolerate unsuitable habitat when site productivity is relatively high than in low productivity areas.

This is the first time that productivity and vegetation structure have been found to be jointly associated with the abundance of the Noisy Miner in woodland remnants. This suggests interplay between available food (as influenced by productivity) and the cost of dominating this food source (as reflected by vegetation structure) in determining the suitability of a site for the Noisy Miner.

A ‘reverse keystone species’ and ‘isoleg theory’

The second primary aim of our study was to gain insight into whether the Noisy Miner was acting as a ‘reverse keystone species’ by affecting the distribution patterns of other avifauna, in particular, potential competitors (i.e. small birds with a high dietary level of overlap with the Noisy Miner), by displacing them into, or restricting their distribution to, less productive areas.

We found strong evidence to suggest that the Noisy Miner displaces, or restricts, certain avifauna to less productive areas. We found that when the abundance of the Noisy Miner was low, perceived competitors (e.g. honeyeaters with a body mass less than the Noisy Miner; small insectivores with conspicuous foraging behaviour such as fantails), occurred in highest abundances at more productive sites. However, when the abundance of the Noisy Miner was high, we found such birds to be most abundant in less productive sites (see Table 2; Fig. 3). Birds with a different diet to the

Noisy Miner (e.g. granivores and carnivores) and large-bodied birds did not show this pattern. Such birds are not the primary focus of Noisy Miner aggression. Indeed, large honeyeaters ($P = 0.06$) were less likely than small honeyeaters ($P < 0.001$) to display a shift in abundance from high productivity sites to low productivity sites with an increasing abundance of the Noisy Miner. ‘Isoleg theory’ involves the identification of a behaviourally dominant species, which, as its density increases in superior habitats, reduces numbers of subordinate species, which congregate in poorer habitats (see Mac Nally and Timewell 2005). Ford (1979) similarly theorised a dominance hierarchy for Australian honeyeaters in which the largest species aggressively defend the best nectar resources with smaller honeyeaters either adopting special behaviours (inconspicuousness or flocking) to obtain access to better flowering sites or using poorer flowering areas. We suggest that as a behaviourally dominant species, the Noisy Miner adheres to ‘isoleg theory’ and the dominance hierarchy described by Ford (1979), such that it actively excludes perceived competitors from productive sites which are richer in food resources. Aggressive behaviour in sites of low productivity may not be warranted. Furthermore, across our study region, sites in unproductive areas tend to be more structurally complex due to less intense land use (e.g. less grazing and firewood removal) and environmental factors (e.g. rockier sites support more shrubs). As previously mentioned, the Noisy Miner would expend a greater proportion of available energy to detect and dispel ‘intruders’ from these environments, which are poorer in food supplies.

Conservation recommendations and conclusions

We have shown that both site productivity and vegetation structure are important predictors of Noisy Miner abundance within woodland remnants. This result is encouraging as previous studies, such as by Oldland et al. (2009), which found that productivity was the sole driver of Noisy Miner habitat occupancy, suggested that manipulation of vegetation structure may do little to prevent Noisy Miner occupation of productive woodland remnants. Our results suggest that increasing the complexity of the vegetation structure (such as by stimulating regrowth and thus high stem densities, planting Acacias and other native

shrubs, and maintaining fallen timber and mistletoe infestations) will help to reduce the suitability of woodland remnants for the Noisy Miner (presumably because it increases the proportion of available energy needed by the Noisy Miner to exclude perceived competitors). For the same reasons, we also recommend that attention be given to maintaining a soft matrix (e.g. an abundance of paddock trees) around woodland remnants. These measures would simultaneously have positive environmental benefits for a broad suite of declining woodland birds (see Montague-Drake et al. 2009).

Our results suggest that wherever possible, restoration works should begin in the most productive areas, as these are the areas where Noisy Miner habitat occupation has the most serious effects for other avifauna. Our results also suggest that while increasing structural complexity of a remnant (and its surrounds) will always help reduce the suitability of a remnant for occupation by large numbers of the Noisy Miner, the level of structural complexity will need to be increased with increasing productivity. Hence, tree spacing will need to be shorter and stem density greater in plantings conducted in productive parts of a landscape.

Our results also suggest that the Noisy Miner may be affecting the long-term survival and reproductive success of perceived competitors by displacing or restricting them to less productive areas. Within our study region, productive areas not only offer more abundant food, but also more temporally-stable food supplies—an important consideration given Australia's highly variable climate (Lindenmayer et al. 2005). It is interesting to note that our data suggests the Noisy Miner 'problem' is driven by the density rather than the presence of this aggressive bird (e.g. see Fig. 3). This is in contrast to other studies which have shown that once a site has Noisy Miners present, small birds are lost (e.g. Piper and Catterall 2003; Hastings and Beattie 2006; Maron 2007). Further studies to understand the factors underpinning this density-driven, rather than presence/absence, response in our study area would have important insights for conservation management.

Piper and Catterall (2003) described the Noisy Miner as a 'reverse keystone species'. Our results provide empirical evidence for this statement. Simberloff (1998) stated that identification of keystone species and the mechanisms that cause them to have

such wide-ranging impacts would almost certainly derive information on the functioning of the entire ecosystem that would be useful in its management, and suggests that some keystone species themselves may be appropriate targets for management. This is almost certainly true for the Noisy Miner.

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