Despotic, high-impact species and the subcontinental scale control of avian assemblage structure

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Abstract. Some species have disproportionate influence on assemblage structure, given their numbers or biomass. Most examples of such "strong interactors" come from small-scale experiments or from observations of the effects of invasive species. There is evidence that entire avian assemblages in open woodlands can be influenced strongly by individual species over very large areas in eastern Australia, with small-bodied species (<50 g) being adversely affected. We used data from repeated surveys in 371 sites in seven districts across a region from Victoria to Queensland (>2000 km). A series of linked Bayesian models was used to identify large-bodied ($\geq$50 g) bird species that were associated with changes in occurrence and abundance of small-bodied species. One native species, the Noisy Miner (*Manorina melanocephala*; family Meliphagidae), was objectively identified as the sole large-bodied species having similar detrimental effects in all districts, depressing occurrence of 57 of 71 small-bodied species. Adverse effects on abundances of small-bodied species were profound when the Noisy Miner occurred with mean site abundances $\geq$ 1.6 birds/2 ha. The Noisy Miner may be the first species to have been shown to influence whole-of-avifauna assemblage structure through despotic aggressiveness over subcontinental scales. These substantial shifts in occurrence rates and abundances of small-bodied species flow on to alter species abundance distributions of entire assemblages over much of eastern Australia.

Key words: avian assemblages; Bayesian model selection; body size; despotism; eastern Australia; hyper-aggression; Manorina melanocephala; *open woodlands; species abundance distributions; species distribution models; strong interactors.*

INTRODUCTION

Strongly interacting species ("strong interactors") are those with a disproportionate influence on local assemblage structure (Paine 1992). Their influence (positive or negative) on assemblage dynamics is much larger than expected based on their numbers or even their biomass. Such taxa have attracted various names, of which "keystone" perhaps is the most pervasive (Menge et al. 1994). Many of the clearest examples of this have arisen when novel species assemblages are produced by human-assisted invasive species (Soulé et al. 2005). Impacts of strongly interacting invasive species can cascade through entire ecosystems (Green et al. 2011). In these cases, the influence of the invader often is manifested by high abundances, blanket cover (e.g., para grass *Brachiaria mutica*, zebra mussel *Dreissena polymorpha*) or great biomass, in which case they may be more appropriately regarded as invasive ecosystem engineers (Jones et al. 1997). We avoid these common

terms, which invariably create contention (Simberloff 1997), and instead focus on the theme of strong interactions among native species.

Although interspecific interactions play out at local scales (home ranges or territories), we were interested in determining whether strong interactions occur in consistent ways over very large domains, in areas as large as a sizeable fraction of a continent. That is, can strong interactors exert intense effects on assemblages over very extensive spatial domains?

Notwithstanding the importance of the ecological phenomenon in its own right, there are at least two other reasons for identifying and measuring assemblage-wide impacts of widespread, potentially strong interactors. These relate to the rapid development of thinking about species abundance distributions (SADs) (McGill et al. 2007) and of species distribution models (Guisan and Zimmermann 2000). There is a rich debate about the relative importance of neutral processes (largely dispersal) and ecological interactions or species adaptations in shaping SADs (Hubbell 2001, McGill et al. 2007, McGill and Nekola 2010). Neutral theory assumes roughly equal per capita demographic characteristics of species and little influence of interspecific interactions

on SADs. Strong interactors, if these occur, clearly have the capacity to affect the local SAD greatly, and would be expected to negate the influence of neutral processes. The existence of strong interactors also may diminish substantially our capacity to build informative habitat suitability maps based on in-site attributes (Yen et al., *in press*) or on landscape variables (Thomson et al. 2007). Such model building has become one of the most active areas of conservation ecology (Guisan et al. 2006). There is a general assumption that species respond only to variation in habitat or to broadscale geographic signals and are at equilibrium, neither of which is likely to be true if strong interactors are present (Elith and Leathwick 2009). The presence of strong interactors may cause a given species to be absent or in reduced densities in habitats that otherwise would be highly suitable.

A well-known example of a strong interactor (of which we believe very few have been reported) is the Brown-headed Cowbird (*Molothrus ater*) of North America, which is a broadly distributed brood parasite on small passerines (Arcese et al. 1996, Morrison and Hahn 2002). However, interspecific aggression is also a likely mechanism through which strong interactors might operate, especially where aggressive defense of resource-rich territories occurs. When strong interactors affect whole assemblages through agonistic behavior, they are regarded as "despotic" species (Mac Nally et al. 2000). Several groups of nectarivorous birds, rodents, and coral reef fish greatly affect assemblage structure through interspecific aggression, typically with larger species excluding smaller ones from higher-quality sites (Brown and Munger 1985, Robertson and Gaines 1986, Robinson and Terborgh 1995, Mac Nally and Timewell 2005). However, most work on such phenomena is limited to relatively local scales (hectares rather than thousands of square kilometers). Therefore, it is unclear whether native "despots" (a term we now use in this sense) that exert an influence over large geographic scales are rare, or whether data have not been sufficiently focused on this particular issue to detect such broad effects.

A potential candidate despot is a native Australian passerine, the Noisy Miner *Manorina melanocephala*, family Meliphagidae (mean body mass ~63 g; Piper and Catterall 2003). The species reportedly has substantial influence on many local avian assemblages in a variety of districts of eastern Australia (Dow 1977, Mac Nally et al. 2000, Piper and Catterall 2003, Clarke and Oldland 2007, Maron 2007, Taylor et al. 2008, Eyre et al. 2009). This species appears to exert a powerful influence on the occurrence and numbers of small-bodied species (<50 g), mostly passerines, by virtue of its intra-colonial cooperation and its hyper-aggressiveness. Experimental removal of the Noisy Miner may lead to recolonization of small remnants of native habitat by small-bodied species in some, but not all, cases, probably depending on the proximity of habitats from which small-bodied species might recolonize (Grey et al. 1997, 1998).

Although the story of this widespread, apparent despot appears to be well documented, there are at least two limitations. First, there has been a focus on *demonstrating* the adverse effects of the Noisy Miner on small-bodied species rather than on assessing objectively whether this particular species is the only, or even the primary, despot driving perturbations in avian assemblages. Second, there are disparate reports on the phenomenon from several districts scattered across eastern Australia (Dow 1977, Mac Nally et al. 2000, Clarke and Oldland 2007, Maron et al. 2011), so there is a need to provide a synthetic meta-analysis in which a large compendium of assemblage data from across the region is treated consistently to evaluate the pervasiveness of effects.

Our questions were as follows. (1) Is variation in effective species richness of small-bodied birds linked to the prevalence of candidate despots without specifically restricting attention to one species (e.g., Noisy Miner)? (2) Are there threshold densities at which the effects of any despots become important and produce widespread change in assemblage structure?

METHODS

Study districts

The study region was the woodland belt of eastern Australia, from western Victoria to central Queensland (Fig. 1). Within this region, we compiled data for 351 sites located in seven study districts. The climate ranges from temperate to subtropical, and average annual rainfall is between 409 mm (Dimboola, Wimmera district) and 630 mm (Injune, Carnarvons district). The dominant woodland types are: buloke *Allocasuarina luehmannii* (Wimmera, 31 sites); *Eucalyptus* spp. (Victorian box-ironbark, 38 sites; Carnarvons, 75 sites); brigalow *Acacia harpophylla* (Moree, 35 sites; Tara, 84 sites; Dalby/Chinchilla, 48 sites); and white cypress pine *Callitris glaucophylla* and spotted gum *Corymbia citriodora* (Barakula, 40 sites). Descriptions of habitat structure are given elsewhere (Mac Nally et al. 2000, Maron et al. 2011). The districts have been modified to differing degrees, predominantly for agriculture. The most modified district is the Wimmera, and the least modified are Barakula and the Carnarvons, where almost all of the original extent of native vegetation remains but was historically subject to cattle grazing and selective timber removal.

Bird surveys

Bird surveys were conducted during the morning and late afternoon in one 2-ha (200 × 100 m) plot at each site. Between three and nine repeat 20-min surveys were conducted depending on the study district. Surveys were conducted in different years in the districts: (1) Wimmera, 2004–2005; (2) Victorian box-ironbark, 1995–1997; (3) Carnarvons, 2007–2008; (4) Moree, 2007–2009; (5) Tara, 2005–2009; (6) Dalby/Chinchilla,
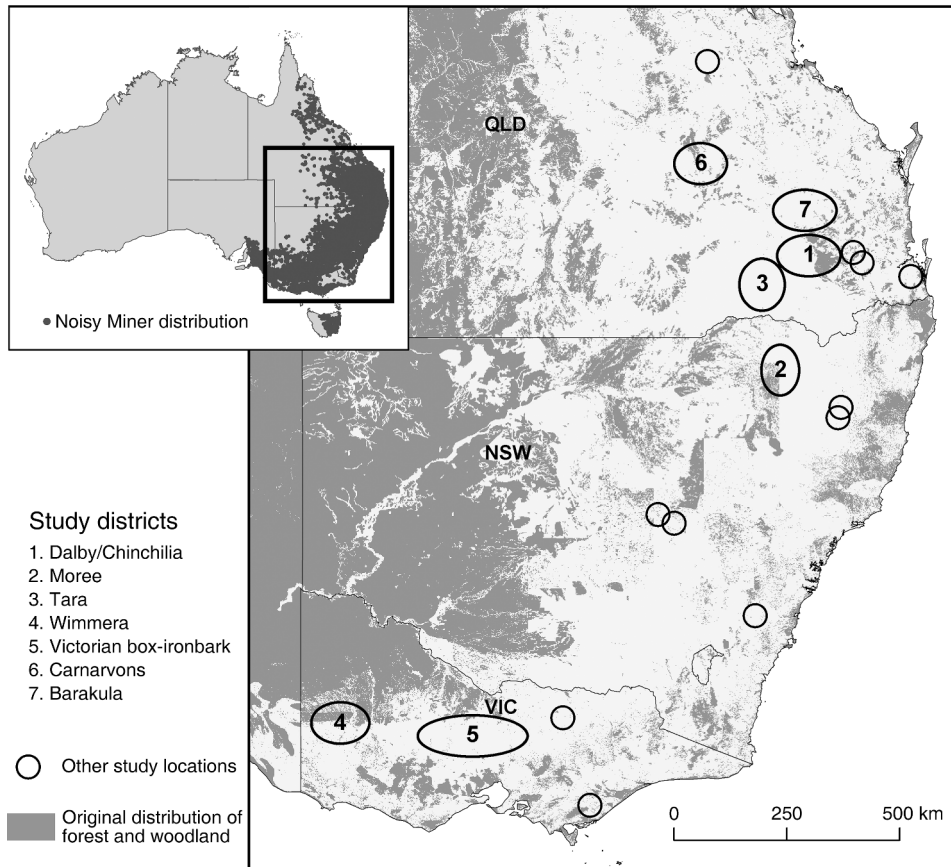
F<small>IG</small>. 1. Main map: locations of study districts across eastern Australia (numbered ovals) with the original extent of forests and woodlands shown in light gray. Locations of other studies reporting negative effects of Noisy Miners on avian assemblages are indicated by open circles; these are listed elsewhere (Maron et al. 2011). Inset: position of the region of the main map in Australia and the distribution of Noisy Miners (solid circles).

2008; and (7) Barakula, 2005–2006 (Mac Nally et al. 2000, Maron et al. 2011).

During each survey, the observer slowly walked the centerline of the plot and all birds within and below the canopy in the plot were recorded. Birds flying above the canopy were included if they appeared to be using the habitat of the plot (e.g., aerial foraging, e.g., Tree Martin *Petrochelidon nigricans*). Although different observers undertook these surveys, we believe that the outcomes will be little affected by observer differences for three reasons. First, all of the woodlands are open habitats with little occlusion by foliage. Second, all observers were experienced ornithologists and had spent much time in these woodlands prior to the surveys being undertaken. Last, our main model (Eq. 1) has a random effect for districts, which incorporates observer differences.

Species exclusions

Data were excluded for (1) water birds and (2) any species occurring at <5 sites across the region. The latter cut-off was arbitrary, but we tried other values (<7, <10

sites) with little effect on inferences. Four exotic species were recorded, but none was found in more than 23 sites (6%): (1) Common Myna *Acridotheres tristis* (15 sites); Common Starling *Sturnus vulgaris* (23 sites); (3) House Sparrow *Passer domesticus* (18 sites); (4) European Greenfinch *Carduelis chloris* (1 site); data for exotic species were elided from the data set.

A<small>NALYSES</small>

Framework

The analyses consisted of a linked series of three stages. Stage 1 involved the use of a Bayesian generalized linear model to characterize reporting rates (RRs, the number of presences per number of surveys conducted for each species) of small-bodied bird species across the entire region. We set the limit to "small-bodied" at <50 g, which is about the geometric mean mass of birds excluding seabirds (Gaston and Blackburn 1995) and substantially lighter than the Noisy Miner, our most likely candidate despot a priori. We used a hierarchical model to account for regional differences in mean RRs among districts. We summed the fitted RRs

for each site to give the effective species richness of small-bodied birds that one would encounter at a site on any visit. These effective species richness values (and their uncertainties) were used as the response variable in Stage 2, in which we used reversible jump Markov chain Monte Carlo models (Green 1995, Lunn et al. 2006) to identify which of the large-bodied ($\geq$50 g) species were most strongly associated with these effective species richness values. The small-bodied species clearly could not be included as potential predictors in this stage because these contribute to the response variable. In Stage 3, we used the site-specific abundances of taxa identified in Stage 2 as the potential predictors of changes in the abundances of small-bodied species using Bayesian change-point analysis (Thomson et al. 2010). The purpose was to determine if there were threshold densities of any taxa identified in Stage 2 at which there are profound effects on the abundances of small-bodied species collectively.

Software

All models described were implemented in WinBUGS (Spiegelhalter et al. 2003). A "burn-in" of 20 000 and a sample of 50 000 were used, and model convergence was checked using three chains and Brooks-Gelman-Rubin statistics (Brooks and Gelman 1998).

Models

Given that we sought potential predictor variables from among taxa that differed greatly in abundances, we used RRs in Stages 1 and 2, which give a less biased means of assessing potential importance. However, in Stage 3, we used abundances because the predictors were treated singly; thus the differences in maximum abundances among species were of less importance.

Stage 1: Effective species richness of small-bodied species.—The hierarchical model involved: (1) a mean RR for all small-bodied species across the sampled districts (i.e., the region); (2) a district-specific mean RR for all small-bodied species; (3) site-specific mean RRs for small-bodied species; and (4) random effects for each species in each district (i.e., effects that may differ for the one species in different districts). Reporting rates have binomial distributions, so that the logit transformation is the appropriate link function for this generalized linear model (McCullagh and Nelder 1989). The model was:

$$Y_{ij(k)} \sim \text{Binomial}(\pi_{ij(k)}, S_{j(k)})$$

$$\text{logit}(\pi_{ij(k)}) = \alpha_{j(k)} + \varepsilon_{ij(k)}$$

$$\Re_{j(k)} = \sum_{i=1}^{N_k} \pi_{ij(k)}. \qquad (1)$$

Here $Y_{ij(k)}$ is the number of surveys within which species i was detected in site j, which is nested in district k; $S_{j(k)}$ is the number of surveys conducted in site j; $\pi_{ij(k)}$ is the

"real" but unknown RR for species i in site j; $\alpha_{j(k)}$ is the mean RR for all small-bodied species in site j; $\varepsilon_{ij(k)}$ is a random effect for species i in site j in district k; and $\Re_{j(k)}$ is the estimated effective species richness of small-bodied species in site j. In cases where a species was missing entirely from a district, the cases were given the value "NA" (not applicable) and the same form of prior as listed in Eq. 1 and those that follow. Such cases have $\pi_{ij(k)}$ values imputed for them (these values are consistent with the remainder of the data and model) but these were prevented from influencing the calculation of the model parameters using the cut( ) function in WinBUGS. These estimated values did not contribute to $\Re_{j(k)}$.

Priors are specified with precision parameters rather than with variance parameters in WinBUGS (Spiegelhalter et al. 2003). The priors for Eq. 1 amount to: (a) site-specific parameters and species-specific random effects within districts; (b) district-level hyperparameters; and (c) regional hyperparameters. For (a), priors were:

$$\alpha_{j(k)} \sim \text{Normal}(\alpha_k, \tau.\alpha_k)I(-4,4)$$

$$\tau.\alpha_k = 1/\sigma.\alpha_k^2 \quad \sigma.\alpha_k \sim \text{Uniform}(0.001, 0.1)$$

$$\varepsilon_{ij(k)} \sim \text{Normal}(0, \tau.\varepsilon_k)$$

$$\tau.\varepsilon_k = 1/\sigma.\varepsilon_k^2 \quad \sigma.\varepsilon_k \sim \text{Uniform}(0.001, 0.1) \qquad (2a)$$

where $\tau.\alpha_k$ is the precision parameter for the mean RR of small-bodied species in sites in district k, and $\tau.\varepsilon_k$ is the precision parameter for species in district k. The priors for the standard deviations ($\sigma.\alpha_k$, $\sigma.\varepsilon_k$) arise from one of A. Gelman's recommendations (Gelman 2006). The construction $I(-4,4)$ means that values are constrained to lie between ±4, which is reasonable, and much speeds model convergence (Spiegelhalter et al. 2003). For (b) and (c), priors were:

$$\alpha_k \sim \text{Normal}(\alpha_{\text{reg}}, \tau.\alpha_{\text{reg}})$$

$$\alpha_{\text{reg}} \sim \text{Normal}(0, 1)I(-4,4)$$

$$\tau.\alpha_{\text{reg}} = 1/\sigma.\alpha_{\text{reg}}^2$$

$$\sigma.\alpha_{\text{reg}} \sim \text{Uniform}(0.001, 0.1). \qquad (2b, c)$$

Here α_k are district-level hyperparameters for the mean RR of small-bodied species, which themselves have a distribution with regional mean (α_{reg}) and precision ($\tau.\alpha_{\text{reg}}$) hyperparameters. From this model, the key outputs are the $\Re_{j(k)}$, which indicate the effective species richness of small-bodied species in each site j.

The "importance" of model parameters was assessed using an odds ratio (OR) framework, which is the ratio of the posterior odds to the prior odds. We computed the amount of the posterior probability mass exceeding zero for model parameters of interest ($p_{1,>0}$). For

positive parameters, the posterior odds are $p_{1,>0}/(1 - p_{1,>0})$, so the OR was equal to this, given that the prior odds were uninformative (i.e., unity). For negative parameters, the posterior odds were inverted (i.e., $(1 - p_{1,>0})/p_{1,>0}$). We adopted a relatively conservative OR ≥ 10 as strong evidence that the parameter differed substantially from 0 (Jeffreys 1961).

Stage 2: Linking site-specific effective species richness of small-bodied species to RRs of large-bodied species.— We restricted our attention to the 55 potential predictor species that had mean body masses ≥ 50 g. We assumed that the effects of potential predictors (large-bodied species) were linear with respect to site-specific effective species richness for small-bodied species ($\Re_{j(k)}$). We also assumed that the predictors operated independently of one another (i.e., there were no interactions).

The problem is a commonly encountered one in ecological and conservation modeling, namely, a multiple regression of one response variable ($\Re_{j(k)}$) on a comparatively large number of potential predictors (Mac Nally 2000). Moreover, one might propagate the uncertainties associated with the response variable ($\tau_{\Re_{j(k)}}$) derived from the initial stage in modeling (Eq. 1). That is, the response variables could be treated either as fixed ($\Re_{j(k)}$) or having uncertainty [$\Re_{j(k)} \sim \text{Normal}(\zeta_{j(k)}, \tau_{\Re_{j(k)}})$].

We used Bayesian model selection (Green 1995) to identify potential predictors (i.e., large-bodied species) with the strongest associations with the $\Re_{j(k)}$ of small-bodied species. We used the reversible-jump Markov chain Monte Carlo sampling (MCMC) jump toolkit available as a plug-in (Lunn et al. 2006) for WinBUGS (Spiegelhalter et al. 2003). This algorithm involves "visiting" all possible models in model space (2^Q, where there are Q possible predictors) in proportion to the "support" that that model has from the data. For simplicity, we used the linear function in jump (jump.lin. pred) and we did not permit interactions among predictors. Although a Poisson model may be more appropriate for effective species richness, jump currently does not support Poisson response variables. However, to ensure that values were always nonnegative, we used the $I(0,)$ construction to ensure that values were ≥ 0.

Prior distributions must be specified for all parameters, including the number of possible predictors k; i.e., k is estimated in a fully Bayesian way (Gelman et al. 2004). We used prior distributions limiting the number of potential predictors to <55, and included the possibility of no (included) predictors. We used two limits (L): a severe one of ≤ 10 predictors and a relatively lenient one, being fewer than [number of sites/10] (viz. 30). The prior for k was $k \sim \text{Binomial}(0.5, L)$ where $L = 10$ or 30. The priors were uninformative with respect to each predictor, with equal prior probability $p_0 = (0.5 \times L)/55$ for each potential predictor (Thomson et al. 2010). With this prior, a posterior probability $p_1 = 3(0.5 \times L)/55$ (amounting to 0.273 for $L = 10$ and 0.818 for $L = 30$) corresponds to an odds ratio of 3, which is a threefold increase from the prior odds [$p_0/(1 - p_0)$] to the posterior

odds [$p_1/(1 - p_1)$]. In this case, the odds ratios are measures of the evidence in the data in favor of inclusion of a predictor relative to its exclusion. Values ≥ 3 generally are considered substantial evidence in variable-inclusion assessments such as we used here (Thomson et al. 2010). We also calculated regression coefficients and associated standard deviations (Lunn et al. 2006). To assess the sensitivity to inclusion of uncertainties and the numbers of potential predictors, we report here on four scenarios: for $L = 10$ and for $L = 30$, each with and without uncertainty propagation in values of $\Re_{j(k)}$.

Stage 3: Threshold densities of potential predictors.— We used a hierarchical Bayesian change-point model to identify whether there was a threshold density above which species identified in Stage 2 had important effects on small-bodied species. We made several assumptions. First, we assumed the possible existence of only one change in intercept in the relationships with potential predictors. More complex models involving change-points in both intercept and slope are possible (Thomson et al. 2010), but we felt that this was beyond the scope of the current application. Second, we assumed that the sudden change, if there were one, might differ among districts but still be related to the regional value through a hierarchical structure. Third, we assumed linearity on the log(abundance) scale for both response and predictor variables.

The model was:

$$Y_{ij} \sim \text{Poisson}(\mu_{ij})$$

$$\log(\mu_{ij}) = \alpha_{0j} \lfloor c_{i(k)} - \xi_i \rfloor + \alpha_{1j} \lfloor \xi_i - c_{i(k)} \rfloor. \quad (3)$$

Here Y_{ij} is the abundance of species j in site i, where the latter is nested in district k. We used a Poisson distribution because abundances, being counts, are nonnegative and the variances increase with the means. The floor brackets ($\lfloor \ \rfloor$) are used here to represent the step( ) function in WinBUGS. The value is 1 if the argument is ≥ 0 and 0 otherwise. For a nominally influential (single) species found in Stage 2, $c_{i(k)}$ is the district-specific threshold density (on the log scale) about which the abundances of the small-bodied species change sharply, if there is a sharp change; ξ_i is the $\log(X + 1)$-transformed site-specific abundance of the influential species. The parameters α_{0j}, α_{1j} are the mean log(abundances) for species j at sites with densities of the influential species that are less than $c_{i(k)}$, and greater than $c_{i(k)}$, respectively, for that district.

Most of the parameters are hierarchical and have hyperparameters that are estimated in the modeling. First, the district thresholds (c_k) are modeled as being drawn from a common normal distribution:

$$c_k \sim \text{Normal}(c_\mu, \tau_c)$$

$$c_\mu \sim \text{Uniform}(0.001, 4) \qquad \tau_c = 1/\sigma_c^2$$

$$\sigma_c \sim \text{Uniform}(0.001, 0.5).$$

TABLE 1.   Model 1 estimates of reporting rates (RRs) and effective richness of small-bodied bird species in woodlands of eastern Australia and in seven districts within the region.

Region and district	Total no. sites	RR (mean ± SD)	Effective richness (mean ± SD)
Eastern Australia	351	0.067 ± 0.003	2.58 ± 0.62
Dalby/Chinchilla	48	0.073 ± 0.003	2.13 ± 0.22
Moree	35	0.067 ± 0.003	2.39 ± 0.14
Tara	84	0.060 ± 0.002	3.15 ± 0.30
Wimmera	31	0.098 ± 0.005	2.74 ± 0.12
Victorian box-ironbark	38	0.074 ± 0.003	3.56 ± 0.36
Carnarvons	75	0.056 ± 0.002	2.25 ± 0.14
Barakula	40	0.048 ± 0.003	1.69 ± 0.09

Notes: RR is measured as number of presence observations per number of surveys conducted for a species. The estimated effective species richness for small-bodied species in a site is computed from Eq. 1.

Thus, c_μ is the regional threshold; the maximum of 4 was set based on the maximum log-transformed value in any site (3.8). Second, α_{0j}, α_{1j} have these definitions:

$$\alpha_{Zj} \sim \text{Normal}(\alpha_{Z\mu}, \tau.\alpha_Z) \qquad \alpha_{Z\mu} \sim \text{Normal}(0, 1)$$

$$\tau.\alpha_Z = 1/\sigma_{\alpha_Z}^2 \qquad \sigma_{\alpha_Z} \sim \text{Uniform}(0.001, 1) \qquad Z \in 0, 1.$$

Here $\alpha_{0\mu}$ and $\alpha_{1\mu}$ are the estimated mean log-transformed abundances of all small-bodied species across the seven districts in all sites where the log-transformed abundances of the influential species are below and above the possible thresholds. For each species, we calculated $(\alpha_{0j} - \alpha_{1j})$, which is an estimate of the difference in the densities of species j at sites below and above the threshold. We used the odds ratio inferential framework to assess whether there were important reductions or increases for species (OR $\geq$ 10).

RESULTS

Stage 1: Reporting rates and effective richness of small-bodied species

The mean regional RR for small-bodied (<50g) woodland bird species in these eastern Australian interior woodlands was 0.067 detections per species per site-visit (Table 1). There were substantial differences among districts, amounting to a greater than twofold difference between the highest and lowest rates (Table 1). The means for the two southern districts were greater than for all of the five northern districts (Table 1).

Recall that the effective species richness is the number of small-bodied species that one would probably encounter on any single visit to that a site. The regional mean was 2.58 species (Table 1), with a range between 1.69 and 3.56 species (Table 1). Again, the means for the southern districts usually were greater than those for the northern districts, apart from Tara, the mean of which fell between the two values of the southern districts (Table 1).

Stage 2: Linking site-specific effective species richness of small-bodied species to RRs of large-bodied species

The RRs of 14 large-bodied species were associated with variation in the effective richness of small-bodied

species in one or more of the four combinations of maximum predictors ($L = 10$ or $L = 30$) and with or without uncertainties in effective richness (Table 2). Five species could be discounted immediately because they appeared in three or fewer districts and, therefore, could not provide a pervasive influence across the region (e.g., Australian King Parrot *Alisterus scapularis*, Emu *Dromaius novaehollandiae*). Two other species were selected in only one of the four combinations notwithstanding their being ubiquitous (Black-faced Cuckoo-Shrike *Coracina novaehollandiae*, White-winged Chough *Corcorax melanorhamphos*; Table 2). A similar conclusion held for the less ubiquitous Brown Falcon *Falco berigora*. The Tawny Frogmouth *Podargus strigoides* is an implausible candidate because it is principally a nocturnally active species. Two other ubiquitous or widespread species, the Australian Magpie *Cracticus tibicen* and Bar-shouldered Dove *Geopelia humeralis*, had positive coefficients. This leaves just three species as candidates for strong interaction with the small-bird assemblage: Crested Pigeon *Ocyphaps lophotes*, Magpie Lark *Grallina cyanoleuca*, and Noisy Miner (Table 2).

Stage 3: Threshold densities of potential predictors

Of the three candidate species derived in Stage 2, only one (Noisy Miner) was associated with a strong contrast between densities of small-bodied species above and below the estimated threshold (Table 3). The nominal threshold densities of two species (Noisy Miner, Magpie Lark) were similar (~1.6 birds/2 ha), but the mean difference in abundance of the small-bodied species below and above those thresholds was pronounced in the Noisy Miner [0.26 birds/2 ha (below) vs. 0.10 birds/2 ha (above)] but was in the opposite-to-expected direction for the Magpie Lark [0.17 birds/2 ha (below) vs. 0.20 birds/2 ha (above)] (Table 3). There was a lower threshold (0.89 birds/2 ha) for the Crested Pigeon; the difference in mean abundances was small [0.17 birds/2 ha (below) vs. 0.16 birds/2 ha (above)].

The distributions of changes in abundance of the small-bodied species in sites in which the predictor abundances were below and above thresholds were very different. For the Noisy Miner, there was strong (odds ratio $\geq$ 10, "decreasers") or relatively strong (odds ratio

TABLE 2. Four approaches for identifying candidate large-bodied ($\geq$50 g) bird species that might influence assemblages of small-bodied (<50 g) species, showing the posterior probability of candidate species (p_1), mean regression coefficients, and SDs.

Species	No. districts	(a) $L = 10$, with uncertainty			(b) $L = 10$, no uncertainty			(c) $L = 30$, with uncertainty			(d) $L = 30$, no uncertainty		
		p_1	Mean	SD	p_1	Mean	SD	p_1	Mean	SD	p_1	Mean	SD
Australian King Parrot *Alisterus scapularis*	3	...	...	...	0.98	0.46	0.10	0.965	0.18	0.05	0.99	0.31	0.08
Australian Magpie *Cracticus tibicen*	7	0.45	0.16	0.19	...	...	...	1	0.36	0.09	...	...	...
Australian Ringneck *Barnardius zonarius*	2	...	...	...	0.44	−0.11	0.13	...	...	...	0.86	−0.15	0.09
Bar-shouldered Dove *Geopelia humeralis*	5	0.79	0.19	0.12	0.89	0.52	0.22	...	...	...	0.93	0.36	0.15
Black-faced Cuckoo-Shrike *Coracina novaehollandiae*	7	0.32	0.11	0.18	...	...	...	...	...	...	...	...	...
Brown Falcon *Falco berigora*	4	...	...	...	0.29	−0.06	0.10	...	...	...	...	...	...
Brown Goshawk *Accipiter fasciatus*	3	0.97	−0.16	0.05	1	−0.52	0.06	0.917	−0.14	0.06	1	−0.42	0.06
Crested Pigeon *Ocyphaps lophotes*	6	1	−0.28	0.05	0.64	−0.21	0.17	...	...	...	0.95	−0.19	0.07
Emu *Dromaius novaehollandiae*	1	...	...	...	0.53	−0.14	0.14	...	...	...	0.89	−0.19	0.09
Magpie Lark *Grallina cyanoleuca*	7	1	−0.36	0.06	0.59	−0.21	0.19	1	−0.34	0.06	0.89	−0.22	0.10
Noisy Miner *Manorina melanocephala*	7	0.92	−0.41	0.14	0.95	−0.32	0.09	1	−0.45	0.05	1	−0.32	0.05
Scaly-breasted Lorikeet *Trichoglossus chlorolepidotus*	3	1	0.16	0.06	0.88	0.34	0.15	0.928	0.15	0.06	0.94	0.25	0.10
Tawny Frogmouth *Podargus strigoides*	5	...	...	...	0.79	0.37	0.20	...	...	...	0.86	0.23	0.13
White-winged Chough *Corcorax melanorhamphos*	7	...	...	...	...	...	...	0.969	0.46	0.15	...	...	...

Notes: Approaches were models with (a) at most $L = 10$ predictor species including uncertainties in deviations of site-specific RRs for small-bodied species; (b) at most $L = 10$ predictor species but excluding those uncertainties; (c) at most $L = 30$ predictor species including uncertainties in deviations of site-specific RRs for small-bodied species; and (d) at most $L = 30$ predictor species but excluding those uncertainties. Ellipses mean that the species was not selected by the algorithm under those conditions (e.g. value of L and with or without uncertainty) as a potential candidate species.

TABLE 3. Parameter estimates (mean $\pm$ SD or with 95% credible interval) of threshold density analyses for three potentially influential large-bodied species and summarized responses of 71 small-bodied species to the three species' threshold abundances using odds ratio (OR) criteria.

Parameter or species differences	Noisy Miner	Magpie Lark	Crested Pigeon
A) Parameter estimates for large-bodied ($\geq$50 g) candidate species			
Threshold log(abundance), c_μ	0.95 $\pm$ 0.17	0.96 $\pm$ 0.06	0.64 $\pm$ 0.14
Threshold abundance of large-bodied species (95% CI)	1.58 (0.74, 2.48)	1.61 (1.26, 1.93)	0.89 (0.42, 1.46)
B) Parameter estimates for small-bodied (<50 g) species			
Mean log(abundance) of small-bodied species below the threshold, $\alpha_{0\mu}$	−1.34 $\pm$ 0.11	−1.78 $\pm$ 0.10	−1.76 $\pm$ 0.11
Mean log(abundance) of small-bodied species above the threshold, $\alpha_{1\mu}$	−2.29 $\pm$ 0.13	−1.69 $\pm$ 0.24	−1.82 $\pm$ 0.18
Mean abundance of small-bodied species below threshold (95% CI) †	0.26 (0.21, 0.33)	0.17 (0.14, 0.21)	0.17 (0.14, 0.21)
Mean abundance small-bodied species above threshold (95% CI) †	0.10 (0.08, 0.13)	0.20 (0.13, 0.31)	0.16 (0.11, 0.23)
C) Number of small (<50 g) species affected by the large species			
Decreasers (OR $\geq$ 10) ‡	50 species	3 species	18 species
Near-decreasers (OR $\geq$ 6) ‡	7	7	1
No difference	12	39	28
Near-increasers (OR $\geq$ 6) §	0	0	0
Increasers (OR $\geq$ 10) §	2	22	24

Notes: For all abundances, the scale of measurement is birds per 2 ha. Log(abundance) estimates were derived using Eq. 3 and were fitted in WinBUGS without prior transformation. The three large species were implicated as potentially influential taxa from Stage 2. Values of the large-bodied species were log(abundance + 1)-transformed beforehand.

† Exponentiated values calculated from the software estimates.

‡ $(\alpha_{0j} - \alpha_{1j}) > 0$.

§ $(\alpha_{0j} - \alpha_{1j}) < 0$.

≥ 6, "near-decreasers") evidence of a decrease above the Noisy Miner threshold density for 57 of the 71 species; abundances of 12 species were similar, and only two (Striated Pardalote *Pardalotus striatus*; Little Lorikeet *Glossopsitta pusilla*) were greater (Table 3). The distribution for the Crested Pigeon was relatively symmetrical, with 19 species being decreasers or near-decreasers and 24 being increasers (Table 3). Higher densities of the Magpie Lark were associated with higher densities of many species (22), and only 10 species were decreasers or near-decreasers (Table 3).

We deduce that the Noisy Miner alone had a regionally significant impact on the occurrence and abundances of small-bodied bird species across this vast region of eastern Australia. This is shown clearly in ordered plots of mean abundances at sites at which the Noisy Miner occurred in densities < 1.58 birds/2 ha compared with sites with Noisy Miner densities ≥ 1.58 birds/2 ha (Fig. 2).

The densities of Noisy Miners associated with substantial differences in the mean abundances of small-bodied species differed by a factor of three among districts. The details are, in ascending order of means: (1) Victorian box-ironbark: 0.80 Noisy Miners/2 ha (95% credible interval, 0.26–1.47); (2) Wimmera: 0.83 (0.23–1.57); (3) Barakula: 1.19 (0.63–1.78); (4) Dalby/Chinchilla: 2.01 (1.66–2.16); (5) Moree: 2.16 (2.01–2.32); (6) Carnarvons: 2.16 (1.69–2.65); and (7) Tara: 2.42 (2.40–2.44). Thus, fewer Noisy Miners produced similar effects in the Victorian box-ironbark and Victorian Wimmera compared with districts such as Moree, Carnarvons, and Tara.

DISCUSSION

The importance of interspecific biotic interactions such as agonistic behavior for the spatial structuring of faunal assemblages has been an important topic for many years (Murray 1981, Schoener 1982, Mac Nally 1983, Robinson and Terborgh 1995). The consistent pattern that we document here indicates that the presence of one despotic species can result in very large-scale shifts in assemblage composition. Throughout the study region, widespread and pronounced assemblage-level effects were linked to the presence, even in relatively low densities (threshold ~1.58 birds/2 ha), of a single native bird species, the Noisy Miner. The mechanism appears to be cooperative interspecific aggression, often involving mobbing (Dow 1977, Grey et al. 1997, Piper and Catterall 2003). Despite screening all large-bodied species, none had a similarly consistent and strong relationship with the abundances and occurrences of small-bodied birds at subcontinental scales. This supports the contention that the Noisy Miner is a despot across a very extensive spatial domain in eastern Australia.

Causality

Distinct patterns of co-occurrence or exclusion are suggestive of biotic interactions (Diamond 1973).
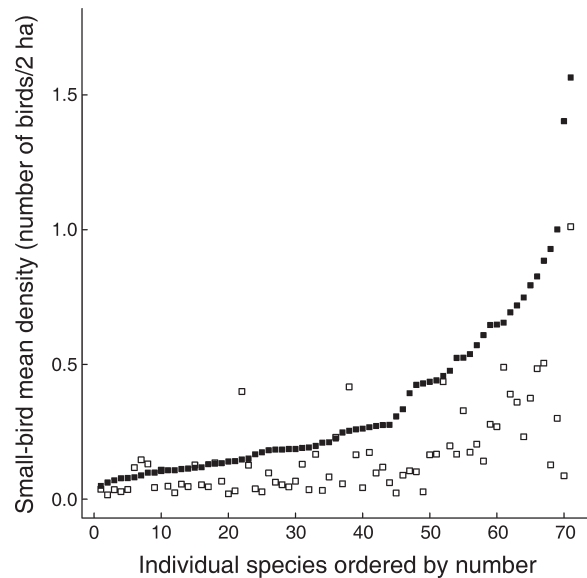

FIG. 2. Mean densities of small-bodied bird species in sites at which the density of Noisy Miners was below the change-point value (solid squares) sorted in ascending order, and the corresponding mean densities of the same ordered set of species in sites at which the density of Noisy Miners was above the change-point value (open squares). The ordered list of species is in the Appendix.

Nevertheless, the interpretation of such patterns is fraught (Stone and Roberts 1990, Gotelli 2000). Their attribution to past or present biotic interactions has been controversial because the experimental demonstration of direct causality, particularly while retaining "real-world" characteristics of a system, is very difficult (Power et al. 1988, Mac Nally 1995, 2001), especially at the scales over which we worked ($>10^6$ km^2). For example, the patterns of occurrence of two species could differ if they were limited by different key resources. Thus, negative correlations in abundances may reflect negative correlations in resource availabilities. Patterns of co-occurrence may reflect subtle, but important, differences in habitat preferences, which in turn may reflect adaptation to past competition (Connell 1980). Biotic interactions also can be mediated through complex chains, or webs, of causation, such as apparent competition mediated by shared predators or parasites (Bonsall and Hassell 1997).

In the case of the Noisy Miner, the evidence of a direct causal link between territorial aggression and the reduced incidence of small-bodied species is strong. The mechanism of exclusion (physical aggression, often by coalitions of Miners) is well-documented (Dow 1977, Maron 2009). The outcomes of sanctioned removal experiments and unsanctioned culls reveal the substantial recovery of the small-bodied component of bird assemblages following the removal of Noisy Miner colonies, at least at small scales (several hectares) and provided that there are nearby sources of recolonists

(Grey et al. 1997, 1998, Debus 2008). At local scales, the independent effect of Noisy Miners on smaller birds typically is an order of magnitude greater than that of habitat characteristics (Maron et al. 2011). Where Noisy Miners are present, their effect on the bird assemblage swamps that of habitat factors such as patch area and vegetation structure (Loyn 1987, Piper and Catterall 2003, Maron 2007). The species is present and dominates small birds throughout both fragmented and intact districts. Last, although the Noisy Miner itself responds to variation in habitat structure and geometry, the drivers of Noisy Miner densities differ geographically. For example, floristics determine Noisy Miner presence in some districts, whereas habitat structure is more important in others (Maron 2007, Howes and Maron 2009, Kath et al. 2009). Nevertheless, the response of small-bodied birds to Noisy Miners is consistent. Thus, there is little doubt that the Noisy Miner directly shapes avian assemblages.

Despotic species and habitat selection

Rather than being a case of interspecific territoriality against close competitors, a much-traveled road in community ecology (Diamond 1973, Wiens 1989), the regional-scale phenomenon that we document is strong interactivity with pronounced assemblage-wide effects. The Noisy Miner's aggression has been referred to as "indiscriminate" (Dow 1977). The Noisy Miner aggressively depresses the densities of >80% of small-bodied bird species. The affected species include not only confamilial taxa (although not congeners) but also unrelated species and those with very different resource use. The Noisy Miner is aggressive toward large-bodied bird species and even non-avian taxa, although interactions with larger bird species are less likely to result in effective displacement from sites (Piper and Catterall 2003, Maron 2009). Nevertheless, it is clear that the Noisy Miner's "target image" is broad enough, or indiscriminate enough, to encompass a large proportion of potential co-occupants of these woodlands.

The strong interactivity of Noisy Miners is an extreme case of despotic habitat selection, in which competitors are excluded from a territory, allowing almost exclusive access to high-quality resources. Such a strategy yields potentially greater and more rapid rewards than increasing exploitation efficiency (Case and Gilpin 1974), particularly for species with a physical advantage over subordinates such as larger body size, group-living, and cooperative defense (Persson 1985, Robinson and Terborgh 1995). This despotic control of assemblage composition may have important cascading effects on ecosystem function, for example, through altered patterns of predation on insect herbivores (Ford and Bell 1982, Loyn et al. 1983). Examples of near-despotic habitat selection occur among many groups of birds, fishes, amphibians, mammals, and crustaceans (Pimm et al. 1985, Robertson and Gaines 1986, Yaron et al. 1993, Robinson and Terborgh 1995, Marvin 1998, Gherardi

and Cioni 2004), although rarely with the same pronounced degree of assemblage-wide effects or over vast areas.

Despotic species and models of species distributions

The construction of models for species distributions has immense importance for biogeography (Dormann 2007), climate-change effects (Thomas 2010), conservation planning (Fleishman et al. 2002), invasion biology (Loo et al. 2007, Schmidt et al. 2010), and restoration ecology (Thomson et al. 2009). To have faith in the reliability of such models, one must be able to either discount or accommodate the influence of strong interactors. The effect of a highly aggressive species, such as the Noisy Miner, will be to reduce the apparent importance of habitat variables in the occurrence of individual bird species (Maron et al. 2011). Researchers interested in determining which habitat variables are important should avoid sites where Noisy Miners are common. In planning to reconstruct landscapes for increasing the probabilities of species' persistence (Mac Nally 2008), a failure to account for the strong interactor in habitat-based model building may lead to inappropriate and costly investments.

Despotic species and species abundance distributions (SADs)

Despotic species have a pronounced effect on the species abundance distributions of individual sites, rendering many species (especially small-bodied ones) much more rare than they would be in the absence of the despotic species (at least, at densities below the threshold density). Moving beyond the distributional fitting of SADs to develop theoretical understanding has been a recent major enterprise (McGill et al. 2007). A series of new directions has been considered, including the influence of sampling scales (Magurran 2007, Sizling et al. 2009), the use of measures other than abundance (e.g., biomass) (Morlon et al. 2009, Henderson and Magurran 2010), guild or functional groupings (Magurran and Henderson 2003) and, most recently, relating SADs directly to environmental gradients (Foster and Dunstan 2010). To our knowledge, the profundity of the impacts of despotic species on SADs has not been considered. The ever-more rich models of SADs need to recognize the potential of despotic species to add "noise" to models and to lessen our apparent understanding.

of Zoology, University of Cambridge, where all of the analyses and much of the writing for this paper were done. Bill Laurance suggested the term "competitive despots," which is used here. We appreciate the comments of Hugh A. Ford and two other reviewers for clarifications in the manuscript. This paper is contribution #232 from the Australian Centre for Biodiversity, Monash University.

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Supplemental Material

Appendix

The ordered list of small-bodied species referred to in Fig. 2 (*Ecological Archives* E093-058-A1).