

The control of rank-abundance distributions by a competitive despotic species

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Abstract Accounting for differences in abundances among species remains a high priority for community ecology. While there has been more than 80 years of work on trying to explain the characteristic *S* shape of rank-abundance distributions (RADs), there has been recent conjecture that the form may not depend on ecological processes per se but may be a general phenomenon arising in many unrelated disciplines. We show that the RAD shape can be influenced by an ecological process, namely, interference competition. The noisy miner (*Manorina melanocephala*) is a hyperaggressive, ‘despotic’ bird that occurs over much of eastern Australia (>10⁶ km²). We compiled data for bird communities from 350 locations within its range, which were collected using standard avian survey methods. We

used hierarchical Bayesian models to show that the RAD shape was much altered when the abundance of the strong interactor exceeded a threshold density; RADs consistently were steeper when the density of the noisy miner ≥ 2.5 birds ha⁻¹. The structure of bird communities at sites where the noisy miner exceeded this density was very different from that at sites where the densities fell below the threshold: species richness and Shannon diversity were much reduced, but mean abundances and mean avian biomass per site did not differ substantially.

Keywords Bayesian models · Colonial birds · Community structure · Hyperaggression · Strong interactors

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Introduction

The quest to understand the reasons for the wide disparity in relative abundances in ecological communities has continued for eight decades (Motomura 1932; Fisher et al. 1943; Preston 1948; McGill et al. 2007; Locey and White 2013). There have been many phenomenological explanations, but mechanistic explanations for the form and variation of the characteristic *S*-shaped curve shape of rank-abundance distributions (RADs) remain elusive (e.g. MacArthur 1957; Preston 1962; Sugihara 1980; Tokeshi 1993; Hubbell 2001; Ulrich et al. 2010; Yen et al. 2013).

Some recent work has attempted to explain RADs [or, equivalently, species-abundance distributions (SADs)] by using very few constraints, typically the total number of individuals (N_0) and the number of species (S_0) (Harte 2011; White et al. 2012; Locey and White 2013). Once N_0 and S_0 are given, RADs are derived from either combinatoric calculations (Locey and White 2013) or from

maximum entropy, or ‘maxent’, methods (Harte 2011), although the latter also requires total metabolic rate (E_0) to be specified, but this is integrated out of the derivation (White et al. 2012). The combinatoric methods involve the calculation of the number of partitions of N_0 objects among S_0 sets, or, in ecological terms, the partitioning of N_0 individuals among S_0 species. Each numerically distinct set is a ‘macrostate’ consisting of multiple ‘microstates’ that are ordered differently. The ordering is not important but the expected shape is thought to be a macrostate near to the centre of the distribution of feasible macrostates (Locey and White 2013). The maximum entropy method generates a log-series that is a function of N_0 and S_0 (Harte 2011).

RAD-like curves appear in many non-ecological guises, suggesting that these curves may not be peculiar to ecological communities per se (Nekola and Brown 2007). Several recent papers have questioned whether there is an ecological basis for the RAD shape (Sizling et al. 2009; White et al. 2012; Yen et al. 2013). Conformance with the most likely macrostate or the most common microstate contingent on given N_0 and S_0 does not necessarily mean that ecological processes are not influential. Conversely, patterns that differ substantially from the expected combinatoric state cannot be attributed easily to ecological mechanisms (Locey and White 2013). The same arguments apply for the maxent derivations.

We think that there needs to be a distinction drawn between two questions regarding RADs. First, are the S -shaped RAD curves peculiar to ecological communities or are these a statistical artefact commonly encountered in a wide range of biotic, abiotic and human contexts? Second, are the parameters of the S -shaped RAD curve influenced by ecological processes given that the S -shaped curve is the expected shape for reasons not specifically related to ecological processes? Our results refer only to the second question, namely, that ecological processes can modify the values of RAD shape parameters; we cannot say whether the S shape is of an ecological origin per se and it is unclear how curve fitting could resolve this issue. Therefore, we do not attempt to explain the near-ubiquitous S -shaped RAD curve but to describe variation in the parameters of RAD curves that are demonstrably due to an ecological process, in this case, interference competition. We use the term ‘shape’ here in the sense of sets of parameters that describe a fitted curve rather than different functional forms of the shape. Therefore, for our purposes, shapes differ if the parameter sets differ substantially rather than, for example, that one of the many differing forms of RAD (Tokeshi 1993) better ‘explain’ the observed data (Mac Nally 2007).

Our focus is on ‘strong interactors’, which are species that have a disproportionately greater effect on local community structure than would be expected given the interactors’ abundances (Paine 1992; Mac Nally et al. 2012). Thus, strong interactors would be expected to alter community

characteristics, including RADs. Some human-assisted invasive species are good examples of strong interactors (Lowe et al. 2004; Green et al. 2011). The trophic cascade is an ecological phenomenon where strong top-down interactions control community structure (Shurin et al. 2002). Most reports of strong interactors are for systems that are relatively limited in area (e.g. individual islands or small lakes), but there is evidence that strong interactors have influence over much greater areas (Mac Nally et al. 2012, 2014). We have not been able find other instances linking the effects of strong interactors to the structure of RADs.

One class of strong interactors is ‘despotic’ species, which affect whole communities through aggressive, agonistic behaviour (Mac Nally et al. 2000). Community structure is much modified by the effects of interspecific aggression in many taxonomic groups (Brown and Munger 1985; Robertson and Gaines 1986; Robinson and Terborgh 1995; Mac Nally and Timewell 2005). One despotic species that has profound effects on whole bird communities is a native Australian honeyeater, the noisy miner *Manorina melanocephala* Latham (Maron et al. 2013). This colonial, sedentary bird species exerts a powerful influence on the occurrence and numbers of small-bodied bird species (<50 g, mostly passerines; the noisy miner has a mean body mass of ca. 63 g) over vast areas of eastern Australia (1.3×10^6 km²; Fig. 1) by virtue of its intra-colonial cooperation and hyperaggression (Maron et al. 2013). In previous work, we established that the effects on small-bodied birds increased sharply once the density of the noisy miner exceeds a threshold (Mac Nally et al. 2012; Thomson et al., in review), so that we had expectations that there may be a threshold effect on RADs too.

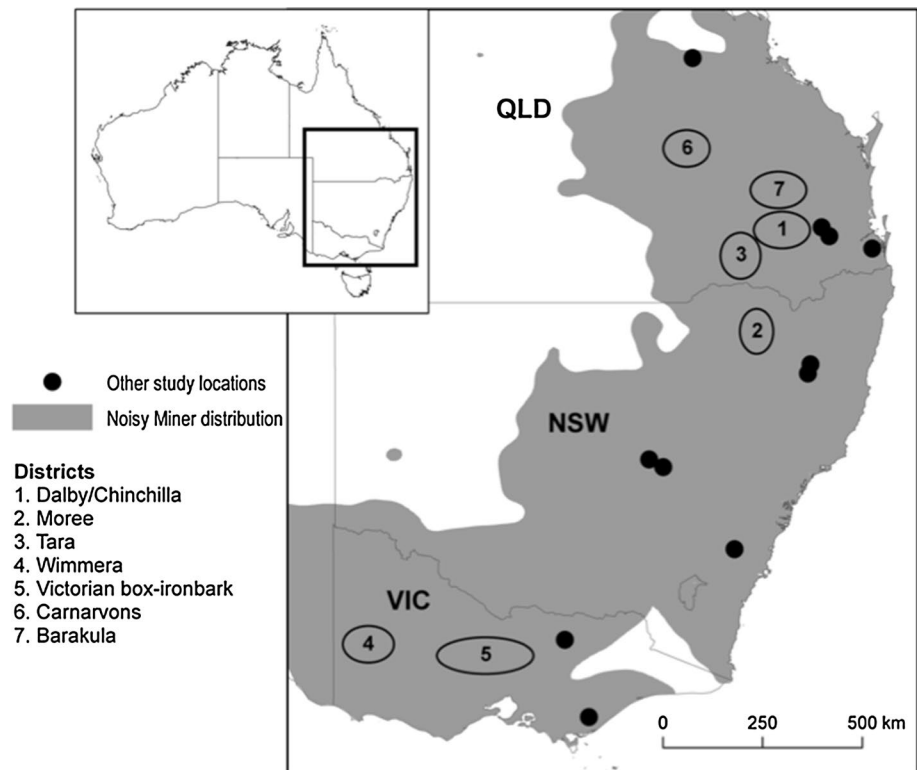
We used hierarchical Bayesian models to account for possible spatial variation in effects and to allow the data to ‘select’ whether there were different RAD shapes as a function of the density of noisy miners. The latter ranged from 0 to >20 birds ha⁻¹, so there was ample scope to explore whether this despotic species induces differences in the parameter values of RADs. Our main questions were: (1) are there one or more statistically derived density thresholds of the noisy miner above which the noisy miner’s influence causes a profound change in RAD shape? (2) If such a threshold exists, what are the effects on avian community characteristics such as species richness, Shannon diversity, abundance and biomass?

Materials and methods

Bird surveys

Surveys were conducted using the standard BirdLife Australia 2nd atlas standard protocols (Barrett et al. 2003).

Fig. 1 Main map: locations of study districts across eastern Australia (numbered ovals) with the distribution of the noisy miner on mainland Australia shown in grey. Locations of other studies reporting negative effects of noisy miners on avian communities are indicated by closed circles; these are listed elsewhere (Maron et al. 2011). *Inset* Position of region on main map of Australia



All 350 sites in the seven districts (a district is a survey area covering tens of thousands of ha; Fig. 1) were visited between three and nine times and data were based on means and SDs of bird abundances from these visits (Online Resource 1).

Modelling: general strategy

RADs typically have a reverse-sigmoidal shape on the log scale, with a steep decline in log relative abundance among the first few most-abundant species, a shallower slope for most of the species (intermediate abundances), and then another steep slope for the rarest of species. The RADs were modelled with multi-knot (here two knots or inflexion points) splines to emulate the S shape of RADs (Botts and Daniels 2008). We chose this approach because we did not want the a priori selection of a form of RAD model (e.g. the RAD corresponding to the log-normal, log-series, zero-sum multinomial, etc.) to influence our inferences. Thus, the RADs were flexible, fitted curves with no implicit underlying model.

We statistically explored whether there was evidence for one or two thresholds by comparing three sets of models based on the densities of noisy miners: no threshold, one threshold, and two thresholds. These amounted to having only one group (i.e. no effects of noisy miners), having two groups of sites in which densities of noisy miners were above or below a data-driven threshold, or having three

groups, where sites were grouped into low densities, moderate densities and high densities of noisy miners, again driven by the data.

Fitting RADs

All densities were the mean species-specific values calculated over all visits to a site. The site-specific species' densities were scaled relative to the most abundant species at the site. Species' values were sorted from the most to least abundant for each site. All curves were anchored at 0 [=ln(1)] on the ordinate for the first species. We used a hierarchical Bayesian model that concurrently modelled all site-specific, two-knot splines. The model accounted for district-specific variation and differences between above- and below-threshold sites. We describe the model for the one-threshold case, but the adjustments for the zero-threshold or two-threshold versions are straightforward. The model (1) was:

$$R_{sj(k)} \sim N\left(\psi_{sj(k)}, \sigma_{R_{sj(k)}}^2\right)I(0, 1);$$

$$\begin{cases} \psi_{sj(k)} \sim N(\rho_{sj(k)}, \sigma_{\epsilon}^2)I(0, 1); \sigma_{\epsilon} \sim U(0, 1) \\ \log(\rho_{sj(k)}) = \alpha_{j(k)} + \beta_{1mk}s + \beta_{2mk}(s - \kappa_{1m})_+ + \beta_{3mk}(s - \kappa_{2m})_+ \end{cases}$$

'N()' means normally distributed and 'U()' means uniformly distributed. The model consists of an observation model (1st line, accounting for uncertainties

in species' relative abundances) and a process model (in brace). Here, s is the s th most abundant species in site j , and site j is nested in district k . $R_{sj(k)}$ is the ratio of the s th most abundant species in site j to the most abundant species at that site [constrained to (0, 1)], and $\sigma_{R_{sj(k)}}^2$ is the corresponding observed variance in values from the multiple surveys. The 'I(minimum, maximum)' construction enforces bounds; for example, $0 \leq \psi_{sj(k)} \leq 1$. Uncertainty is propagated by modelling the ratio with each species' site-specific SD, scaled by the mean of the most abundant species at that site. $\psi_{sj(k)}$ is assumed to be a realization of the true ratio for the s th most abundant species in site j , which is modelled on the log scale $[\rho_{sj(k)}]$ as a function of species position on the RAD (s). For each site j , the model is estimated from $s = 1 \dots S_{j(k)}$, which is the number of species observed in that site. The key parameters are the intercepts $[\alpha_{j(k)}]$, three slopes per curve ($\beta_{1:3}$) and two knots per curve ($\kappa_{1,2}$). The m index signifies whether the site is a below-threshold ($m = 1$) or above-threshold ($m = 2$) site. The form $(.)_+$ means 0 if the argument is <0 , and 1 if the argument ≥ 1 . Therefore, the three regression coefficients ($\beta_{1:3}$) apply to those parts of the curve in which $s < \kappa_1, \kappa_1 \leq s < \kappa_2, s \geq \kappa_2$, respectively (Botts and Daniels 2008). The hierarchical structure is implemented through the priors for the model parameters. These are:

$$\begin{aligned} \alpha_k &\sim N(\alpha_{\text{region}}, \sigma_{\alpha, \text{region}}^2); \alpha_{\text{region}} \sim N(0, 9); \\ \sigma_{\alpha, \text{region}} &\sim U(0.001, 2); \kappa_{1m} \sim U(1, \kappa_{2m}); \\ \kappa_{2m} &\sim U(\kappa_{1m}, M = 25); m \in 1, 2; \beta_{lm, \text{region}} \sim N(0, 9)I(0, 0); \\ \sigma_{lm, \text{region}} &\sim U(0.001, 2); l \in 1, 2, 3; m \in 1, 2. \end{aligned}$$

The knots are constructed such that the first is less than the second, and the second is given a maximum possible value of 25. The latter is a high number but is not the maximum number of species in any one site.

How many thresholds (zero, one or two)?

We undertook a series of analyses to establish whether the sites differed in their RADs with respect to the densities of noisy miners. First, we fitted just one model (i.e. $m = 1$ for all sites) to determine whether having a threshold is justified statistically. Second, we allowed for two sets of sites differing in being above and below a threshold of noisy miner densities, and we conducted a sensitivity analysis with sites partitioned into two groups based on the different mean densities of the noisy miner. The threshold densities used were: 0, 0.4, 0.8, 1.6, 2, 2.5, 3, 3.5, 4.25, 5, 7.5, 10 and 15 noisy miners ha^{-1} . We fitted model 1 using each of these thresholds and obtained a measure of model fit,

the deviance information criterion (DIC) (Spiegelhalter et al. 2002). We used the Ando correction (Ando 2007) to DIC (Bayesian predictive information criterion; BPIC) to account for possible overfitting. The threshold value associated with the lowest BPIC value is the best fit to the data. To distinguish among values, we used the relative probability of minimizing information loss of model k compared to the model with minimum BPIC, namely $\Pr(\text{model } k) = e^{(\text{DIC}_{\text{minimum}} - \text{DIC}_k)/2}$ (Burnham and Anderson 1998). Third, we considered the possibility of two thresholds and hence three groups of sites. We computed the BPIC scores for the 78 combinations of 0, 0.4, ... 15 noisy miners ha^{-1} , which have more estimable parameters than the zero- or one-threshold models so BPIC is necessary for discrimination.

All models were fitted by using WinBUGS (Spiegelhalter et al. 2003). Parameters were estimated from three Markov chain Monte Carlo (MCMC) chains of 30,000 iterations after 10,000 iteration burn-in periods (results discarded). We checked MCMC mixing and convergence by examining chain histories, auto-correlation plots and Gelman-Rubin-Brooks statistics (Brooks and Gelman 1998).

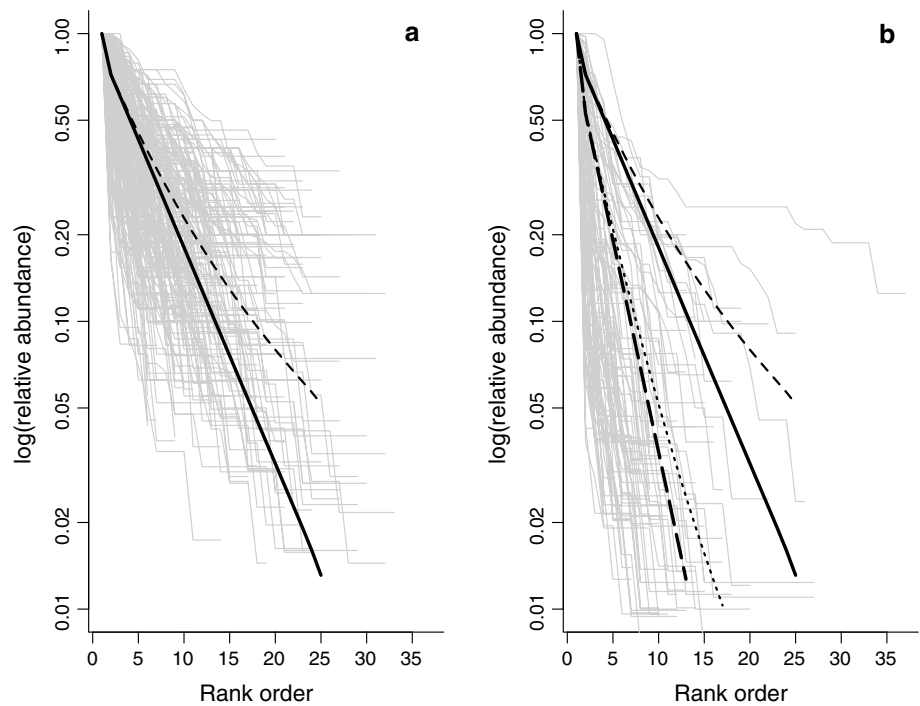
Community composition

We first omitted the data for noisy miners from the community matrix of mean bird densities. The matrix was converted into a distance matrix using the Bray-Curtis index, which was used in a non-metric multidimensional scaling ordination using metaMDS in the *vegan* package in R (Oksanen et al. 2006). The resulting ordination was correlated with the density of noisy miners using *envfit* in the *vegan* package in R (Oksanen et al. 2006) with 9,999 permutations. Once a threshold was identified (see "Results"), sites were allocated to sets in which the density of the noisy miner was below and above the threshold. Comparisons of these sets for species richness, Shannon diversity indices, abundances and biomasses were by standard *t*-tests with random effects for districts and assuming Gaussian error distributions.

Results

There was compelling statistical evidence for at least one threshold; the information criterion score for the no-threshold model was 71 units more than the minimum for a threshold model (at 2.5 noisy miners ha^{-1}), corresponding to a probability of $<10^{-16}$. The threshold at 2.5 noisy miners ha^{-1} had a score 4.6 units less than the next smallest score (2.0 noisy miners ha^{-1}), so that the 2nd-best model had a probability relative to the best of ca. 0.1 (Online Resource 2). There were two 'best' two-threshold

Fig. 2 Rank-abundance distributions (RADs) illustrating the influence of the noisy miner on entire communities. **a** RADs for all sites with mean noisy miner density <2.5 birds ha^{-1} (pale grey); solid line is the median computed two-knot spline, dashed line is the mean computed two-knot spline. **b** RADs for all sites in which the mean noisy miner density ≥ 2.5 birds ha^{-1} (pale grey); long-dashed line is the median computed two-knot spline and the dotted line is the mean computed two-knot spline. Median (solid lines) and mean (short-dashed lines) for sites with sub-threshold densities of noisy miners (a) are shown for reference



models (with threshold pairs at 2.5 and 4.0, and at 2.5 and 10 noisy miners ha^{-1} ; Online Resource 3). The models with these pairs of thresholds had information-criterion scores that were ca. 2.1 units less than the best one-threshold model, which differ little statistically from the one-threshold model (probability ca. 0.35). For parsimony, we used a one-threshold model with a threshold of 2.5 noisy miners ha^{-1} .

The mean and median RADs for sites with fewer than 2.5 noisy miners ha^{-1} (Fig. 2a) were substantially shallower than the corresponding mean and median RADs for sites with ≥ 2.5 noisy miners ha^{-1} (Fig. 2b). Details of the mean fitted splines for the sites below and above the threshold of 2.5 birds ha^{-1} are listed in Table 1. The initial slopes from the anchored point (1, 0) were substantially shallower for the below-threshold sites (mean -0.149 vs -0.337), and the first knot point was 1.27 vs 6.17. The 2nd (-0.015 vs -0.026) and 3rd (-0.037 vs -0.581) slopes were steeper for the above-threshold sites.

The composition of the bird communities was strongly correlated with the density of noisy miners ($0.52, P < 10^{-4}$) (Fig. 3). There was little overlap between sites in ordination space with <2.5 noisy miners ha^{-1} and sites with ≥ 2.5 noisy miners ha^{-1} , and there was a very pronounced difference between sites from which noisy miners were absent and those with high densities of noisy miners (Fig. 3).

Species richness ($t_{348} = 5.23, P < 0.001$; Fig. 4a) and Shannon diversity indices ($t_{348} = 12.12, P < 0.001$; Fig. 4b) were significantly higher in below-threshold sites than in above-threshold sites, but the total bird abundance (birds

Table 1 Statistics (mean \pm SD) for the parameters of the two-knot splines for sites with <2.5 noisy miners ha^{-1} and for ≥ 2.5 noisy miners ha^{-1}

Parameter	<2.5 Noisy miners ha^{-1}	≥ 2.5 Noisy miners ha^{-1}
Slope 1 (β_{1m})	-0.149 ± 0.066	-0.337 ± 0.083
Slope 2 (β_{2m})	-0.015 ± 0.007	-0.026 ± 0.016
Slope 3 (β_{3m})	-0.037 ± 0.036	-0.581 ± 0.424
Knot 1 (κ_{1m})	1.27 ± 0.25	6.17 ± 3.12
Knot 2 (κ_{1m})	24.11 ± 0.86	22.87 ± 2.01

m index signifies whether the site is a below-threshold ($m = 1$) or above-threshold ($m = 2$) site

ha^{-1}) ($t_{348} = -1.1, P \sim 0.23$; Fig. 4c) and total avian biomass (kg ha^{-1}) ($t_{348} = -0.53, P \sim 0.6$; Fig. 4d) did not differ greatly. Data for the noisy miner were included in these calculations.

Discussion

Ecological processes appear to be able to influence the parameter values of RADs and a suite of characteristics of avian communities over vast areas of a continent. The RADs were much steeper when the density of the competitive despot, the noisy miner, exceeded 2.5 birds ha^{-1} (Fig. 2). The highly coordinated and persistent interspecific aggression of the noisy miner appeared to induce profound shifts in community composition, both in the occurrence of species and in their relative abundances.

At sufficiently high densities, the despotic species had a marked effect on the parameters of the RADs of individual sites.

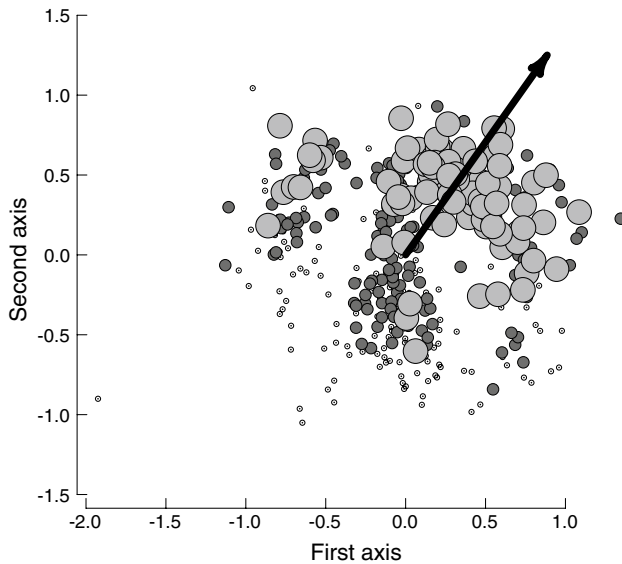
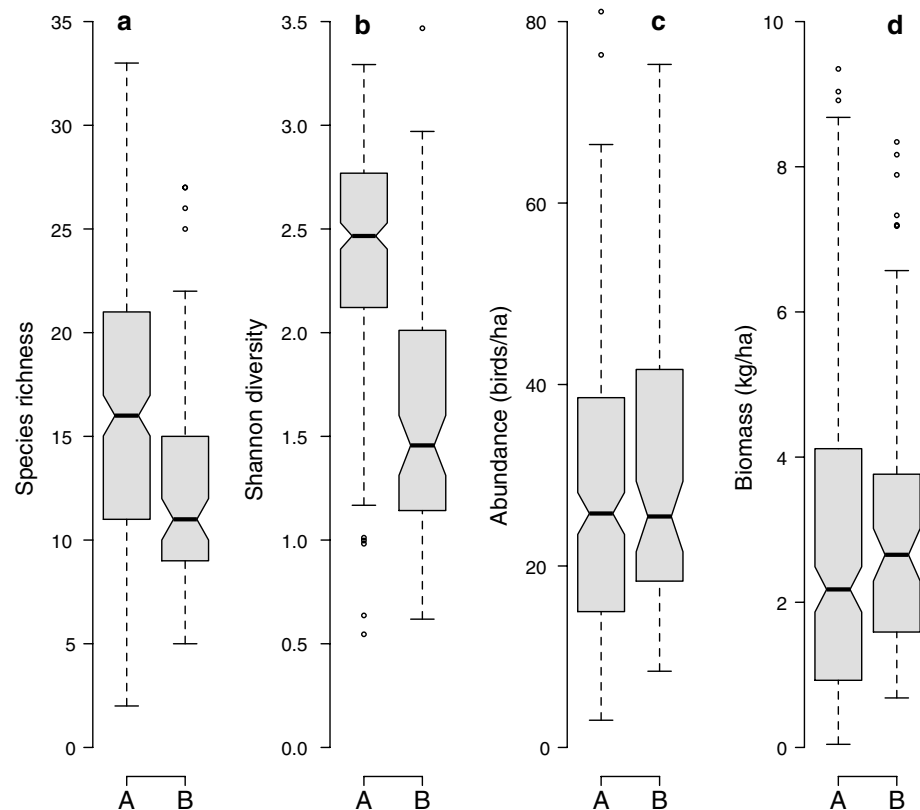


Fig. 3 Ordination of bird communities (excluding the noisy miner) with sites coded by size and greyscale [≥ 2.5 noisy miners ha^{-1} (large mid-grey circles), < 2.5 noisy miners ha^{-1} (medium-sized darker grey circles), no recorded noisy miners (small open circles with central dots)]. Thick arrow indicates the correlation between the ordination and the density of noisy miners ($r = 0.52$, $P < 10^{-4}$ by permutation)

Fig. 4 Notched box plots of contrasts between sites with below-threshold densities [< 2.5 noisy miners ha^{-1} ; abscissa (A)] and above-threshold densities [≥ 2.5 noisy miners ha^{-1} ; abscissa (B)] of noisy miners for: **a** species richness, **b** Shannon diversity index, **c** total bird abundance (birds ha^{-1}), and **d** total avian biomass (kg ha^{-1}). Notches are the median values, grey bars are the interquartile ranges (25–75 % of values), dashed lines are ± 2 SD, and small circles are points lying outside ± 2 SD (outliers). Data for the noisy miner are included in these calculations



The similarity in mean abundances and mean biomass showed that the despotism of the noisy miners at densities ≥ 2.5 birds ha^{-1} threshold appeared to drive a ‘reconstruction’ of the bird communities, with a mean loss of 25 % of species (a marked reduction of mean S) but with little change in mean total abundance, N (Fig. 4). Shannon diversity was depressed above the threshold, but the mean total biomass differed little. These results suggest that the effects of the noisy miner were not artefacts of differences in primary productivity among sites because the supported avian biomasses were not consistently different in the above- and below-threshold communities. Other systematic differences in site characteristics do not appear to account for the differences in community statistics (Maron et al. 2011).

The importance of interspecific behavioural interactions, such as agonistic dominance, for the structuring of animal communities has been described for many years (Murray 1981; Schoener 1982; Mac Nally 1983; Robinson and Terborgh 1995; Jankowski et al. 2010; Peiman and Robinson 2010). The noisy miner affects the capacity of small (≤ 63 g) nectarivorous birds from tracking variation in nectar availability at regional scales ($\geq 10,000$ km^2), but does not inhibit large (> 63 g) nectarivorous birds from doing so (Bennett et al. 2014b). The despot also had a similar body-size-specific effect on breeding success: breeding activity and success of birds smaller than the miner are depressed by its occurrence while larger birds are unaffected or even

appear to benefit from the presence of the noisy miner (Bennett et al. 2014a). The noisy miner greatly perturbs the guild structure of avian communities when it establishes colonies of sufficient numbers (Howes et al. 2014).

The noisy miner is a profound example of a perturber of bird communities over an immense area (Maron et al. 2013), but is the effect of the noisy miner a rogue phenomenon? Are other species capable of having such profound effects over such large areas, albeit through other mechanisms? The black-tailed prairie dog *Cynomys ludovicianus* indirectly controls small-mammal communities by modifying habitats over >400 000 km² of the North American prairie (Cully et al. 2010). The herbivorous white-tailed deer *Odocoileus virginianus* controls much of the native vegetation across eastern North America with concomitant effects on the biota (Horsley et al. 2003; Rooney and Waller 2003). Two of the congeners of the noisy miner have similar perturbative effects on avifaunas to the noisy miner. The largely allopatric bell miner *Manorina melanophrys* (Loyn et al. 1983) and the yellow-throated miner *Manorina flavigula* (Mac Nally et al. 2014) influence avifaunas in similar ways to the noisy miner. None of these examples has yet been linked to RADs, but it seems clear that single, strongly interacting species are more common than may be appreciated, and that their influence can extend to at least sub-continental scales (hundreds of thousands to millions of square kilometres).

The influence of the noisy miner probably is the most extreme example yet to be reported of the numerical non-equivalence of species; just 2.5 noisy miners ha⁻¹ were sufficient to induce stark changes in entire avian communities. This hearkens back to the distinctions between the interpretation of food webs by using energy and nutrient flows compared with how one might represent food webs through interspecific dynamics (i.e. per capita competition or predation coefficients in the community matrix) (Paine 1992). Expressing communities as vectors of numbers of different species, or even of their biomasses, provides little information on dynamics, which clearly is shown by the changes in community structure induced by interspecific competition exerted by the noisy miner. This implies that the recent combinatoric and maxent approaches to RADs might need to be modified to account for the numerical non-equality of species in assemblages, especially in their different dynamic effects.

An issue that we think needs to be considered more carefully in RAD and SAD literature is the circumscription of a ‘local community’. There appears to be a lack of critical attention to the spatial and temporal extent of what constitutes a local community. For birds, many communities on continents at any point in time [e.g. a standard North American Breeding Bird Survey route (Sauer et al. 2005)] are relatively temporary assemblages of species,

with each species having its own idiosyncratic spatial and temporal dynamics (Mac Nally 1995). Even closely related congeners may be quite dissimilar, ranging from seasonal migrants to regional nomads to year-round residents within the one genus (e.g. the Australian whistlers *Pachycephala* spp.) (Griffioen and Clarke 2002). A consequence of this range of dynamics is that the communities change ‘kaleidoscopically’ over landscape to regional scales at sub-annual time frames (Mac Nally and McGoldrick 1997), which are much shorter than the lifetimes of the birds (Yom-tov 1987). While birds collectively are likely to be the most absolutely mobile of terrestrial organisms, similar kinds of heterogeneous dynamics occur for other organisms commensurate with their levels of mobility (Bonnet et al. 1999).

A more complete understanding of RADs would explain how the numbers of species and Shannon diversity could change so dramatically due to a despot’s influence yet leave the total numbers of individuals and total biomass of birds in local communities essentially unchanged. While the despotic miner almost certainly is a beneficiary of freed resources, it is not a very large bird (ca. 63 g) so that its numerical increase alone does not explain the near parity in biomass among the sites in the below- and above-thresholds sets. There appears to be some equilibrating process(es) involving many species becoming redistributed over large scales (landscapes to regions) coupled with in situ population dynamics. Broadly speaking, the unified neutral theory of biodiversity and biogeography (Hubbell 2001) treats the local communities as being embedded within a meta-community, and allows for transmission of individuals among local communities. It seems hard to reconcile this theory with profoundly different RAD shapes in nearby locations that differ mainly in the abundance of a single species.

Our approach was based on general curve fitting rather than fitting as a way to assess conformance with the many models that have been proposed. Attempting to infer process or mechanism by conformance with different distributions does not provide a critical advance in our understanding of why abundance distributions are as they are (McGill 2003). Numbers alone do not appear to be sufficient and the topic could be more closely aligned with other areas of ecology. Differences in abundances need to be understood in terms of landscape and regional context (e.g. meta-community dynamics), differences in energy and nutrient use, and as functions of species-specific interaction rates given the effects we have described here.

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