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Noisy neighbours and myna problems: Interaction webs and aggression around tree hollows in urban habitats

Andrew M. Rogers[1,2] 🔳 | Andrea S. Griffin[3] | Berndt J. van Rensburg[2,4] | Salit Kark[1,2]

[1]The Biodiversity Research Group, The School of Biological Sciences, The University of Queensland, Brisbane, QLD, Australia

[2]Centre for Biodiversity and Conservation Science, The School of Biological Sciences, The University of Queensland, Brisbane, QLD, Australia

[3]Animal Behaviour and Cognition Lab, Conservation Science Research Group, School of Psychology, University of Newcastle, Callaghan, NSW, Australia

[4]Department of Zoology, University of Johannesburg, Johannesburg, South Africa

Correspondence
Andrew M. Rogers
Email: a.munro.rogers@gmail.com

Abstract

1. Interaction networks among native and invasive species in a community can inform both invasion impacts and applied management of invasive species. The intensity of aggressive interactions may be related to the overlap in species' ecological niche and functional traits, especially in cavity-breeding species, that often compete for limited nesting sites. Australia is home to over 100 native and introduced cavity-nesting species, including several invasive species that are widespread globally, such as the common myna *Acridotheres tristis*. Here, we aimed to test the extent to which shared functional traits inform the intensity of aggression between cavity-nesting birds.

2. We quantified the outcomes of aggressive interactions between birds in large hollow-bearing trees in SE Queensland, Australia. We examined whether more similarly sized birds interacted more frequently, whether larger species won aggressive interactions more often, and whether cavity-breeding species with similar preferences for nesting sites (breeding-niche space) interacted more frequently.

3. We recorded a total of 410 aggressive interactions and 48 interacting bird species around tree hollows, including 20 cavity-nesting bird species. These interactions were dominated by the invasive common myna, the native noisy miner (a non-cavity-breeder) and the native rainbow lorikeet *Trichoglossus moluccanus*, but the common myna won the largest total number of interspecific interactions. On average, larger birds won aggressive interactions more frequently, yet there were some important exceptions to this finding; the common myna (113 ± 30 g) won 26 of the 29 interactions against the larger native rainbow lorikeet (126 ± 44 g). Importantly, species with more similar nest-site preferences were observed aggressively interacting more frequently.

4. *Synthesis and applications*. The impact of the invasive common myna was higher-site preferences. Control efforts for the myna should focus on birds that nest in natural tree hollows. An analysis of shared traits by managers could be used to help identify how many local species would benefit from common myna control in a given area and test if further behavioural studies of common myna are warranted.

KEYWORDS

Acridotheres tristis, biotic interactions, common myna, competition network, interaction webs, invasive impact, noisy miner, urban ecology

1 | INTRODUCTION

Invasive species can significantly impact native communities through competition for resources (Koenig, 2003; Russell, Sataruddin, & Heard, 2014; Stokes, Banks, Pech, & Spratt, 2009; van Riel, van der Velde, & bij de Vaate, 2009). Competition in the form of direct interactions (aggression) or indirect interactions (e.g. more efficient exploitation of resources) is important to quantify at a community level as such interactions have important consequences for invasion dynamics (i.e. establishment, spread and impact; Hui & Richardson, 2018; Kamenova et al., 2017) as well as community response to disturbance (Battisti, Poeta, & Fanelli, 2016; Ings et al., 2009; Kéfi et al., 2015; LeBrun, 2005; Mokross, Ryder, Côrtes, Wolfe, & Stouffer, 2014). For widespread species, studies of their impact from small parts of their invasive range may not translate to communities with areas of different species assemblages (Koenig, 2003). Within each community, multiple species interacting around resources can create unique complex interaction webs with important implications for management, especially where removing species from a community is being considered (Baker, Holden, Plein, McCarthy, & Possingham, 2018; Charter, Izhaki, Ben, & Kark, 2016).

Competitive interactions are more likely between species that share resources requirements (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012; Kunstler et al., 2012; Reif, Reifová, Skoracka, & Kuczyński, 2018). For birds, such resources can include habitat space, food and nesting sites (Cain & Langmore, 2016; Sol, Bartomeus, & Griffin, 2012; Strubbe & Matthysen, 2009). While competition over non-critical resources such as food may be avoided by small shifts in foraging behaviour (Batalha, Ramos, & Cardoso, 2013), birds compete more strongly over critical resources such as territories and nesting sites (Brazill-Boast, Van Rooij, Pryke, & Griffith, 2011; Ghilain & Belisle, 2008; Minot & Perrins, 1986). Resource requirements are often correlated with species functional traits like body size (Tilman, 2004; Woodward & Hildrew, 2002) and occupied niche space (Brazill-Boast, Pryke, & Griffith, 2010). Such traits can also influence the outcome of competitive interactions; for example, larger species often have a physical advantage in aggressive interactions (Jennions & Backwell, 1996; Miller et al., 2017; Petren & Case, 1996). Therefore, exploring the extent to which trait overlaps between invasive and native birds can provide some insight into which species within a community are more likely to be impacted by the increase in competition from the introduction of an invasive species (Diamond & Ross, 2020; Orchan, Chiron, Schwartz, & Kark, 2013).

The common (Indian) myna *Acridotheres tristis* is one of the world's most successful invasive species having established populations in over 39 countries outside its native range (ISSG, 2010), and its primary impact on native species is aggressive dominance of nesting sites in cavities, both in natural tree hollows and other structures (Charter et al., 2016; Pell & Tidemann, 1997). In Australia, the common myna is widespread occurring from tropics in the north to temperate climates in the southernmost part of the continent (Martin, 1996). However, common myna impacts on native species in Australia have only been reported from a small part of its invasive range (i.e. the state of New South Wales and the territory of Canberra) and it remains unclear how competitive impacts vary across the continent.

Australia has a uniquely high percentage of cavity-nesting birds, with at least 115 species of birds (15% of all Australian bird species), including eight species of invasive birds, using hollows for nesting or roosting (Gibbons & Lindenmayer, 2002). Cavity-nesting species are of conservation concern as the loss of large hollow-bearing trees from modified habitats (Koch, Munks, & Spencer, 2009; Koch & Woehler, 2007; Le Roux, Ikin, Lindenmayer, Manning, & Gibbons, 2014) and the presence of invasive species (Lindenmayer et al., 2017) reduces nesting opportunities in urban habitats (Grarock, Lindenmayer, Wood, & Tidemann, 2013). However, interspecific competition in these studies has mostly been inferred from spatial segregation in nests site locations (Grarock et al., 2013; Pell & Tidemann, 1997), or co-occurrence around potential nest sites (Davis, Major, & Taylor, 2013). Importantly, cavity-breeding birds are an interesting group in which to study the relationship between species traits and competition intensity as: (a) the species nesting requirements are well known (Gibbons & Lindenmayer, 2002; Higgins, 1999) and (b) they are likely to interact around the limited number of potential nesting sites (Davis et al., 2013).

Aggressive interactions are an important process in shaping Australian bird community ecology in part due to the presence of the noisy miner *Manorina melanocephala* (Dhondt & Adriaensen, 1999; Kennedy & White, 1996; Shochat et al., 2010; Tilman, 1982). This bird is a native Australian honeyeater, a colony-nesting, despotic and highly adapted to urban environments (Haythorpe, Burke, & Sulikowski, 2014; Montague-Drake, Lindenmayer, Cunningham, & Stein, 2011). These birds breed cooperatively, and family groups control large territories and exclude most species which are smaller than they are (70–80 g: Howes & Maron, 2009; Maron et al., 2013). The abundance of the noisy miner has changed bird community composition at landscape scales and especially in modified environments (Maron et al., 2013).

To better understand the interaction network around cavities and the impact that invasive species are having on urban cavity-breeding birds, our study aimed to explore how aggressive interactions and their outcomes are related to similarities in body weight and breeding-niche overlap. Body mass is important as larger species are assumed to have an advantage in physical contests (Human & Gordon, 1996; Sol et al., 2012). Breeding-niche reflects, in part, the nesting and habitat requirements for a given species, with increasing overlap in breeding-niche positively correlated with increasing competition (Brazill-Boast et al., 2010; Diamond & Ross, 2020). We predicted that species with increasing overlap in their traits (body size and nest-site preferences) would interact more frequently. We also predicted that the impacts of common myna aggression would be highest for similarly sized species (Diamond & Ross, 2020; Orchan et al., 2013).

2 | MATERIALS AND METHODS

2.1 | Study sites

We quantified interspecific interactions in large hollow-bearing trees at eight sites across southeast Queensland (Figure 1). We selected all study sites based on the presence of large, old eucalyptus trees (most live trees were either *Eucalyptus tereticornis* or *Corymbia maculata*), which had visible hollows and were observable from accessible roads or parks. Hollows were treated as a nesting site if birds displayed behaviours often associated with breeding around them (Manning, Lindenmayer, & Barry, 2004). We visited each site 10 times during the peak breeding months for common mynas from September 2015 to March 2016. The number of trees at each site varied from one to eight. The number of observable hollows in the trees ranged from four to 17. For sites with multiple trees, we found a central location from which the greatest number of trees could be observed simultaneously.

2.2 | Interaction surveys

During a visit to a site, one observer recorded all species that visited the focal trees and all interspecies interactions that occurred within the focal trees for 1 hr (Rogers, 2020). Observers were 10–30 m from the study trees and used 8 × magnification binoculars. We recorded all interactions between two or more species, with interactions defined as one species flying at or coming within 50 cm of another species. Interactions between species like the birds with good eyesight also occur at distances >50 cm, but evaluating and recording such interactions for a large number of wild individuals were not feasible in this study. For each interaction, we recorded the species and the number of individuals involved, which species initiated the interaction and which species was the recipient. For each individual in each interaction, the behaviour was recorded (swoop, contact, chase, fight or physical contact, threat, displace, avoid, vocalization), and an outcome was determined for each species (win, lose). The species which was displaced from its perch or expended the most energy on the interaction was considered the loser of the interaction. For example, interactions in which there was little or no response from the recipient species, the initiating species has expended energy on the interaction and thus we considered it a loss for the initiator and a win for the recipient. If the recipient species showed no response (no alarm call, no movement towards or away from the initiating species), it was considered a 'win' for that species as it has avoided spending energy.

2.3 | Overlap of preferred nesting sites

We calculated the overlap in preferred nesting sites between species using the niche overlap model proposed by Geange, Pledger, Burns, and Shima (2011). This approach can accommodate both categorical
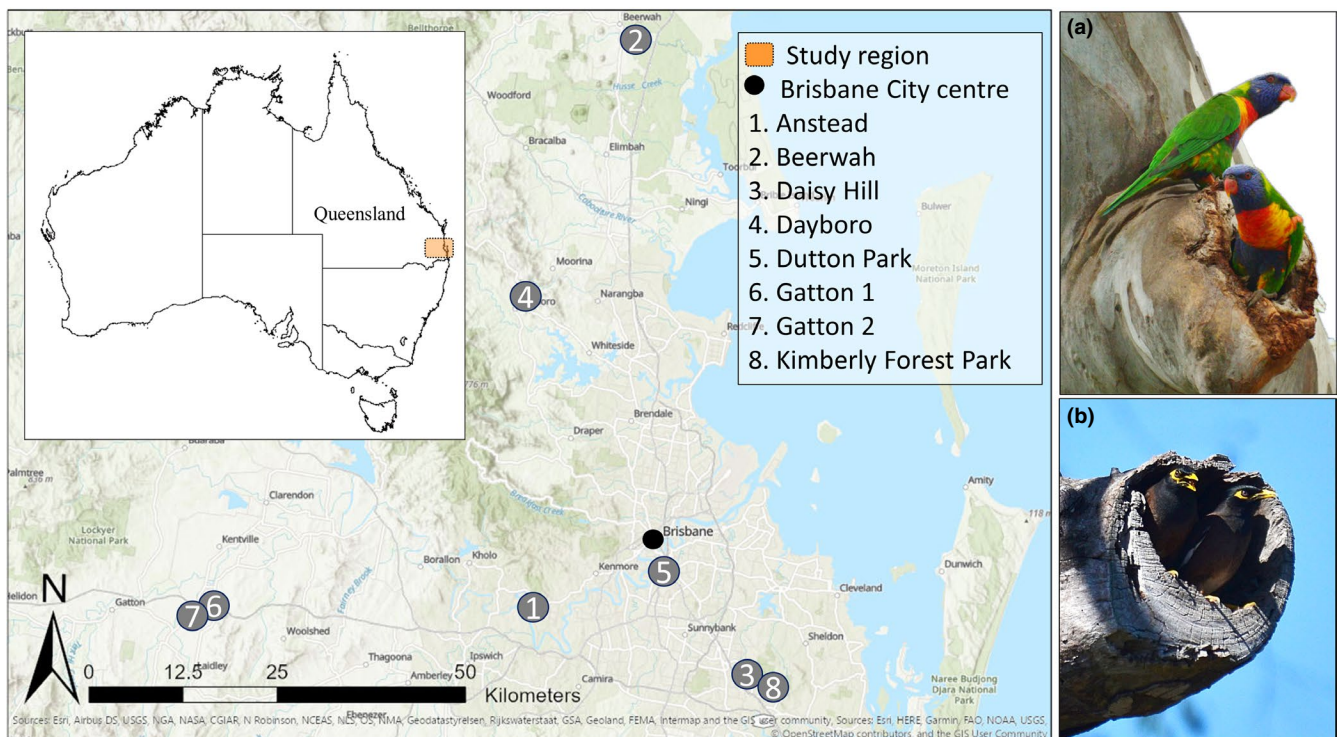

FIGURE 1 Map of the study area and sites in southeast Queensland. At each site, large old trees with visible hollows in use by cavity-nesting species were found. Birds interacting within these trees were recorded with the most frequently observed cavity-nesting species being the native rainbow lorikeet (a) and the invasive common myna (b). Image: ArcGIS basemap. Photos: A. Rogers

and continuous species traits to calculate the niche space occupied by a species. For each interacting species pair, the model calculates an overlap score from 0 to 1 for each trait with 0 representing no overlap in niche space, and a value of 1 being complete niche overlap. Overall niche overlap for each species pair is then calculated using the mean of the overlap of all traits. The statistical significance of the niche overlap is also calculated for each species pair (Geange et al., 2011; Quinn & Keough, 2002).

We compiled species trait data and data on preferred cavity characteristics for 18 of the 20 observed cavity-breeding species. The majority of the data were collected from the Handbook of Australian and New Zealand Birds (HANZAB; Higgins, 1999; Table S1) and Garnett et al. (2015). For species that did not have trait data in the HANZAB, a Google Scholar search was performed with the species common name, species scientific name and the keywords 'nesting', 'nest', and 'breeding'. For species which did not have data on breeding sites or cavity characteristics in published studies, we used data from bird breeders including data on preferred nest box dimensions (see Table S1 for information on trait data and sources). In the niche overlap model, we included the following variables: body mass in grams (min, mean, maximum), cavity entrance diameter in cm (minimum, mean and maximum), breeding months, whether a species was an obligate cavity nester (yes or no) and nesting location (tree hollow, man-made structure, underground burrow).

To examine how niche overlap values are distributed in the observed community we calculated frequency distributions of niche overlap scores for two bird groups: (a) all cavity-nesting birds observed across the sites (including those not observed interacting) and (b) the cavity-nesting species recorded interacting. The total number of niche overlap scores within 10 equal-sized bins with a range of 0.1 (e.g. 0–0.1, 0.1–0.2, ... 0.9–1.0) was summed. We tested the difference between the median niche overlap between the two distributions with a *t*-test assuming equal variance. Additionally, to examine whether birds with higher niche overlap values do indeed show a greater total number of interactions, we calculated the frequency distribution for all the observed interactions between cavity-nesting birds.

2.4 | Analysis of interspecies interactions

To compare aggression between species, we ranked species based on the total interactions (all interactions that species was involved in), the total number of wins, the ratio of wins to losses and the ratio of total wins to total interactions. We also compared the total number of species with which the common myna, the rainbow lorikeet *Trichoglossus moluccanus*, the scaly-breasted lorikeet *Trichoglossus chlorolepidotus* and the noisy miner interacted. For each of these focal species, we calculated the total number of interactions with all other species and the total number of interactions with other hollow-nesting species. To test if the larger species were more likely to initiate and/or win interactions across the entire community, we calculated the body size difference between initiator and recipient,

and winner and loser then took the average body size differences across all observed interactions.

We created interaction network figures using the program 'Gephi' (Bastian, Heymann, & Jacomy, 2009). The network graph was created using the win–lose data for each species pairs with the weighted line between species (nodes) representing the count of interactions which were won by each species (Table S2). Species that won more interactions against another species have a thicker line. We built the observed network by creating a directed edge list in Excel. Each interacting species pair was entered as a row that contained the species that won the interaction, the species that lost the interaction and the count of the number of times the first species won against the second species. The list was then converted to a weighted matrix using the package IGRAPH (Csardi & Nepusz, 2006) in the programing language R (R Core Team, 2015).

We used generalized additive models to explore the relationship between interaction counts, as well as outcome, and species' traits (niche overlap and difference in body size). Models were run for the entire interacting community and for the cavity-breeding species alone. Generalized additive models were used because of the hump-shaped relationship between the total number of interactions and the difference in body size (Zuur et al., 2011). For all analysis of interspecies interactions, we summed interactions across all surveys for each site and included site and the species pair as categorical fixed effects. Mobbing events, interaction events with more than four birds (the max number of birds included one pair of each species) were removed from the analysis of the interactions. Interactions with more than four individuals occurred 44 of 410 observed interactions. We examined the relationship between traits and interactions for two groups: (a) all observed birds and (b) cavity-breeding species. Response variables included 'total interactions' (summed interactions between species pairs), and 'outcome' which was the total number of wins for each species (e.g. the number of times rainbow lorikeet won vs. the common myna). For all models, explanatory variables included 'difference in mean body size', 'site', 'species ID'. We used absolute body size difference as an explanatory variables for the models for total interactions while relative body size difference was used in the models of outcome. For models of cavity-breeding species, we also ran separate models with niche overlap as an explanatory variable. For models with total interactions as a response variable, we used a quasi-binomial family error distribution and a log link function to account for over-dispersion. For the outcome models, we used a binomial error distribution with a logit link function.

3 | RESULTS

3.1 | Interspecific interactions in urban trees

Overall, we surveyed interspecies interactions around natural hollows across eight sites in southeast Queensland, for a total of 80 hr. We observed a total of 25 trees that had a total of 71 observed

hollows. We recorded 4,758 individuals, 75 species and 410 interactions between 48 different species (Figure 2). Most birds, 64% of all observed species, were involved in at least one interaction.

Non-cavity-nesting species were involved in 204 of the 410 total interactions we observed. We found a total of 18 obligate cavity-nesting birds interacting with other species. Cavity nesters were
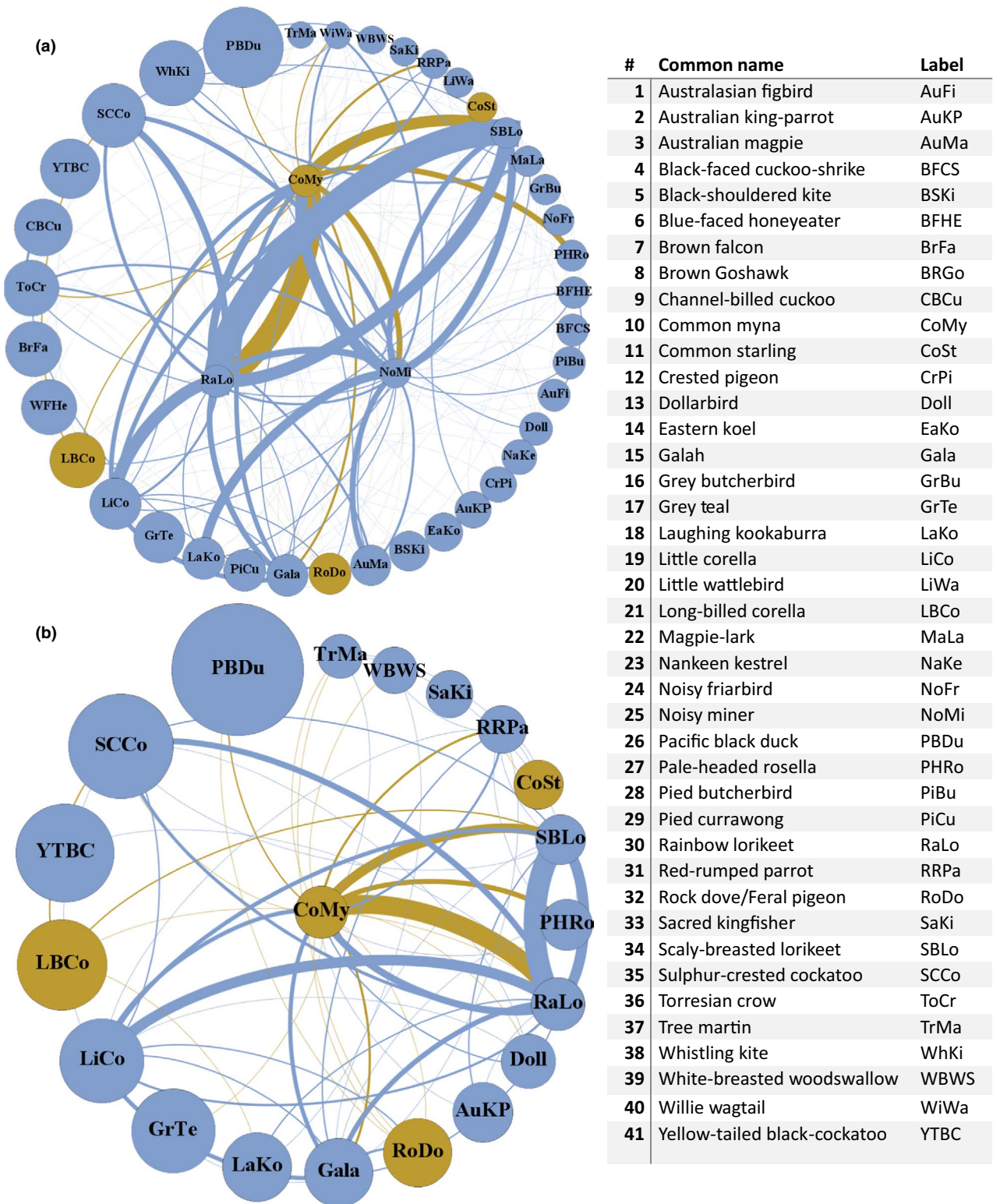

#	Common name	Label
1	Australasian figbird	AuFi
2	Australian king-parrot	AuKP
3	Australian magpie	AuMa
4	Black-faced cuckoo-shrike	BFCS
5	Black-shouldered kite	BSKi
6	Blue-faced honeyeater	BFHE
7	Brown falcon	BrFa
8	Brown Goshawk	BRGo
9	Channel-billed cuckoo	CBCu
10	Common myna	CoMy
11	Common starling	CoSt
12	Crested pigeon	CrPi
13	Dollarbird	Doll
14	Eastern koel	EaKo
15	Galah	Gala
16	Grey butcherbird	GrBu
17	Grey teal	GrTe
18	Laughing kookaburra	LaKo
19	Little corella	LiCo
20	Little wattlebird	LiWa
21	Long-billed corella	LBCo
22	Magpie-lark	MaLa
23	Nankeen kestrel	NaKe
24	Noisy friarbird	NoFr
25	Noisy miner	NoMi
26	Pacific black duck	PBDu
27	Pale-headed rosella	PHRo
28	Pied butcherbird	PiBu
29	Pied currawong	PiCu
30	Rainbow lorikeet	RaLo
31	Red-rumped parrot	RRPa
32	Rock dove/Feral pigeon	RoDo
33	Sacred kingfisher	SaKi
34	Scaly-breasted lorikeet	SBLo
35	Sulphur-crested cockatoo	SCCo
36	Torresian crow	ToCr
37	Tree martin	TrMa
38	Whistling kite	WhKi
39	White-breasted woodswallow	WBWS
40	Willie wagtail	WiWa
41	Yellow-tailed black-cockatoo	YTBC

FIGURE 2 Interaction network showing the total number of interactions between species observed in large, hollow-bearing urban trees. Species are represented as nodes (circles). Interactions between species are lines. Node size is the relative body size of each of the species. Lines are weighted as a proportion of total interactions observed between all species. (a) All observed species with cavity species in the centre ring and non-cavity nesters in the outer ring, (b) only cavity-nesting species. Non-native species are in orange and native species are in blue

involved in 50% of all interactions despite forming only 37.5% of the interacting species pool and 24% of the total observed species pool.

3.2 | The top 10 aggressive birds around cavities

Of the top 10 most frequently interacting species (Table 1), four were non-cavity nesters including the noisy miner, the Australian magpie *Cracticus tibicen*, magpie-lark *Grallina cyanoleuca* and the Torresian crow *Corvus orru*. The noisy miner was the second most frequently observed interacting species, observed in 118 of the total 410 interactions. Noisy miners interacted with 26 other species, which represented 34.6% of the total observed species pool and 54.1% of the interacting species pool. Of all observed interactions, noisy miners were recorded initiating the highest number of interactions, had the second most number of wins (Figure 3) and were the most likely to win an interaction which they had initiated (Table 1). We found a significant positive correlation between a species abundance and the number of interactions it was involved in (Figure S1).

Of the cavity-nesting species, the common myna was involved in the third-largest number of interactions, initiated the second most number of interactions (after the noisy miner), and had the highest number of wins (Figure 3), making it one of the most aggressive cavity-nesting species in absolute terms (Table 1). The rainbow lorikeet and the noisy miner had more total interactions than the common myna, but had fewer total wins (Table 1). Relative to all other species, the common myna was the fifth most successful aggressive species (wins/total interactions; Table 1). The common myna was recorded interacting with more species than any of the native cavity-nesting species (Table 2).
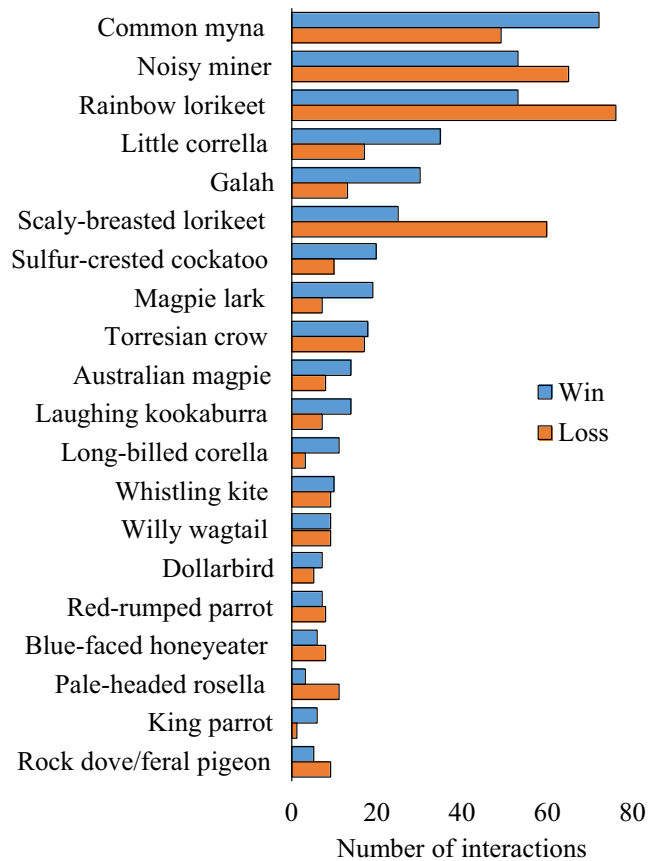

FIGURE 3 The total number of wins and losses in interspecific interactions for the top 20 most frequently interacting species, ranked by the total number of wins. While the native rainbow lorikeet was involved in more interactions, the invasive common myna had the most number of wins

TABLE 1 Species interactions and outcomes around natural hollows for the 10 most frequently interacting species. While rainbow lorikeets were observed interacting the most (total interactions), they did not win as many of the interactions as the common myna (total wins). Based on the wins to loss ratio and wins to total interaction ratio, the common myna is one of the top five most aggressive species

	Interactions		Win		Loss		Initiation		Win/loss		Win/total	
Species	#	Rank	#	Rank	#	Rank	#	Rank	#	Rank	#	Rank
Rainbow lorikeet *Trichoglossus moluccanus*[a]	114	1	38	3	76	1	39	3	0.5	8	0.33	8
Noisy miner *Manorina melanocephala*	110	2	45	2	65	2	84	1	0.69	7	0.41	6
Common myna *Acridotheres tristis*[a]	105	3	56	1	49	4	72	2	1.14	5	0.53	5
Scaly-breasted lorikeet *Trichoglossus chlorolepidotus*[a]	78	4	18	6	60	3	20	6	0.3	9	0.23	1
Little corella *Cacatua sanguinea*[a]	44	7	27	4	17	5	30	4	1.59	3	0.61	3
Galah *Eolophus roseicapilla*[a]	36	6	23	5	13	6	25	5	1.77	2	0.63	2
Torresian crow *Corvus orru*	29	5	12	8	17	5	12	8	0.71	6	0.41	6
Magpie-lark *Grallina cyanoleuca*	25	9	18	7	7	9	15	7	2.57	1	0.72	1
Sulphur-crested cockatoo *Cacatua galerita*[a]	22	8	12	9	10	7	15	7	1.2	4	0.54	4
Australian magpie *Cracticus tibicen*	12	10	4	10	8	8	3	9	0.5	8	0.33	8

[a]Cavity-nesting species.

TABLE 2 Level of aggression towards other species compared to similar sized native species shown for all species and for cavity nesters alone. The common myna showed more aggression towards other species compared to similar sized native species. The myna showed the levels of aggression similar to the highly aggressive native noisy miner

Focal species	All interspecific interactions	Interactions with other cavity-breeders
Common myna *Acridotheres tristis*	23	14
Noisy miner *Manorina melanocephala*	26	11
Pale-headed rosella *Platycercus adscitus*	7	5
Rainbow lorikeet *Trichoglossus moluccanus*	13	10
Scaly-breasted lorikeet *Trichoglossus chlorolepidotus*	15	10

3.3 | Patterns of niche overlap and body size

We calculated the niche overlap for 18 cavity-nesting species resulting in 210 niche overlap scores. Significant niche overlap ($p \leq 0.05$) was found between eight species; and high niche overlap ($p \leq 0.10$) was found between another nine species (Table S3) such that 16 of 18 species had high niche overlap with at least one other species. The common myna showed significant overlap with the pale-headed rosella, and high niche overlap with the common (European) starling *Sturnus vulgaris*, the rainbow lorikeet and the scaly-breasted lorikeet.

The median niche overlap of interacting cavity nesters (0.419 ± 0.13) was higher than species present in the trees but were not observed interacting (0.372 ± 0.12; $df = 100$, $t = 2.048$, $p = 0.022$; Figure 4a). The median niche overlap value for all observed interactions was 0.472 (± 0.12) with 69.3% of observed interactions between cavity-nesting species had a niche overlap value larger than 0.5 (Figure 4a). For all observed cavity-breeding species, 48% of all interactions occurred between species with a niche overlap that had a $p < 0.1$ (Figure 4b). In particular, the common myna interacted most frequently with native species (pale-headed rosella, rainbow lorikeet and scaly-breasted lorikeet) with which it had high niche overlap scores ($p < 0.1$; Table S3).

The body size range for the entire interacting community was 16.6–1,060 g with a median body size of 123 g (Figure S2). Across all interactions, the species initiating the interaction were on average 27.6 g smaller than the recipients, and the species winning the interaction were 51.3 g larger (Figure S3). This result is likely influenced by the high number (110) of interactions initiated by the relatively small noisy miner and common myna. The common myna weighs 113 ± 30 g, and has a body size range that overlaps with 14 native species, including the species with which it most frequently interacted: the noisy miner (71.3 ± 27 g), the pale-headed rosella
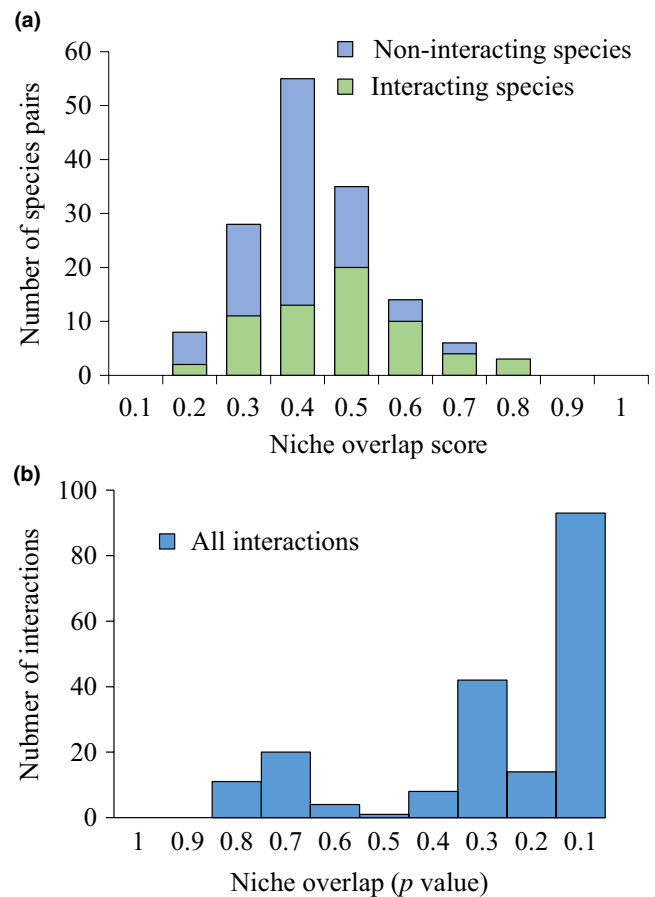
FIGURE 4 Interactions occurred more frequently between species which had a higher niche overlap. The median niche overlap score for (a) birds observed interacting was 0.419 ± 0.13 while birds observed in the trees but did not interact had a score of 0.372 ± 0.12. Additionally, nearly half (48%) of all interactions (b) occurred between species that had niche overlap scores that significance scores above 0.1

(103 ± 99 g), the rainbow lorikeet (126 ± 44 g) and the scaly-breasted lorikeet (86.9 ± 10 g).

3.4 | Traits and interactions

Body size difference showed a positive significant relationship with interaction outcome (edf = 1.05, $F = 14.63$, $p < 0.0002$; Table 3) with larger species winning more interactions. However, body size difference was not a significant predictor of the total number of interactions between species pairs (edf = 2.71, $F = 1.96$, $p = 0.12$; Table 3). When considering only the interactions between cavity-nesting species, neither body size (edf = 2.14, $\chi^2 = 3.62$, $p = 0.28$; Table 3) nor niche overlap (edf = 1.00, $F = 2.12$, $p = 0.15$; Table 3) showed a significant relationship with the total number of interactions between two species. For models of interaction outcome between cavity-nesting species, the difference in body size did not show a significant relationship to whether a species won or lost an interaction (edf = 3.584, $\chi^2 = 7.64$, $p = 0.12$; Table 3).

TABLE 3 Results of generalized additive models exploring the relationship between overlap in species traits and interaction frequency and outcome. We used interactions between all species pairs ('all interactions' = the total interactions between two species), the total number of wins for each species pair as response variables for all observed interactions and for the cavity-breeding community separately. Difference in body size and niche overlap were included as random variables. Site and the species interacting were included as fixed effects

	Response variable	Deviance explained	R^2	Explanatory variables	edf	Ref. df	F	p
All species	Interaction sum	82.5%	0.65	Difference in body size	2.71	3.10	1.96	0.12
				Site	6.52	7.00	50.84	$<2^{-16}$
				Interacting species ID	67.48	147.00	2.11	9.97^{-9}
	Interaction outcome (win/loss)	37.59%	−0.01	Difference in body size	1.05	1.08	14.63	2.22^{-4}
				Site	4.01^{-3}	7.00	0.01	0.44
				Interacting species ID	39.45	157.0	63.91	5.03^{-5}
Cavity-nesting species	Interaction sum	78.3%	0.63	Niche overlap	1.00	1	2.13	0.15
				Site	5.67	7	19.02	1.25^{-9}
				Interacting species ID	25.02	54	2.38	9.97^{-7}
	Interaction outcome (win/loss)	37.9	0.63	Difference in body size	3.58	4.27	7.64	0.115
				Site	2.29	7.00	4.01	0.16
				Interacting species ID	9.98	60.00	13.93	0.07

4 | DISCUSSION

4.1 | Urban interaction networks

We found that birds using large trees in southeast Queensland interact to form a network of both cavity and non-cavity-nesting species, which is dominated by a few highly aggressive species. We found that smaller species lost aggressive interactions more often, supporting previous work (Edworthy, 2016; Haythorpe, Sulikowski, & Burke, 2012; Miller et al., 2017; Sol et al., 2012). However, the difference in mean body size did not predict the outcome of interactions between species pairs. This could be due to high overlap in body size between similarly sized species (Diamond & Ross, 2020). For example, the common myna (113 ± 30 g) won most of the interactions (26/29) with the rainbow lorikeet (126 ± 44 g), the native species closest in size. While the mean bodyweight of the rainbow lorikeet is larger, there is a large overlap in body size between the two species.

Our results suggest that the common myna is one of the most aggressive species in our study area, supporting the idea that much of its ecological impact is related to competition for nest sites. Previous work has shown that the common myna is not more aggressive than native species around food resources (Haythorpe et al., 2012; Lowe, Taylor, & Major, 2011; Sol et al., 2012). In a study of nest box use in Canberra, Grarock et al. (2013) found spatial segregation between common myna and native bird species and attributed that pattern in part to competition, yet direct aggressive interactions were not explicitly quantified. In Sydney, Lowe et al. (2011) also found that mynas occupied few natural tree hollows in remnant forest patches and suggested mynas were no more aggressive than native species. Our work supports the results found by Pell and Tidemann (1997) who found that mynas displayed more aggression and occupied more tree hollows than native species. In North America, Diamond

and Ross (2020) found that mynas competed most strongly with the similarly sized native red-bellied woodpeckers *Melanerpes carolinus* and invasive common (European) starlings. It appears that overlap in body size and cavity preference are key indicators of their impact everywhere they are invasive.

While this study initially focused on the common myna, the native noisy miner was observed in just over a quarter of all interactions. It remains unclear how miner aggression influences tree hollow access at our sites, yet most cavity-nesting species across our sites were similar in size or larger than the noisy miner (71.3 g), which may help them cope with the year-round noisy miner aggression (Mac Nally, Bowen, Howes, McApline, & Maron, 2012). Efforts to improve breeding habitat for small cavity-nesting species should reduce the suitability of surrounding habitat for noisy miners by increasing the structural complexity of vegetation (Eyre, Maron, Mathieson, & Haseler, 2009; Kath, Maron, & Dunn, 2009).

4.2 | Aggression in the cavity-nesting bird community

Five of the 16 native cavity-breeding species we observed interacting have high niche overlap with invasive and feral species highlighting that available niche space in urban areas is becoming more crowded (Batalha et al., 2013; Czajka, 2011; Letten, Keith, Tozer, & Hui, 2015). Across our sites, the common myna interacted most frequently with species with which it had higher overlap in body size and nest-site preferences, but these traits did not predict the specific interspecies interaction frequency or outcome of interactions. This means that while a comparison of traits could inform which native species common myna (and other invasive species) are likely to impact in other communities, the severity of the impact will be

harder to predict. However, given the common myna's dominance over the slightly larger rainbow lorikeet, it seems that the impact of the common myna will be greater than would be assumed by comparisons of body size alone.

4.3 | Management and conservation implications

Current control efforts focus on trapping birds in urban areas. However, such efforts are unlikely to reduce local populations of mynas (Grarock, Tidemann, Wood, & Lindenmayer, 2014) and therefore are not suitable to reduce their primary impact of competition for nest sites. While mynas have shown some preference for nesting in artificial structures (such as buildings; Lowe et al., 2011), efforts to reduce the impact of common mynas should focus on targeting individual mynas that nest in tree hollows. While behavioural studies of competition can be time and resource-intensive, managers could compare trait overlap between species that occur in an area to help inform whether local control is worthwhile or further behavioural studies are warranted. Control of individual birds at the nest cavity can utilize a range of live traps and other approaches developed for the study of cavity-nesting species (Braga, Shibuya, Cerboncini, & Roper, 2014; Stanback & Koenig, 1994; te Marvelde, Webber, van den Burg, & Visser, 2011).

AUTHORS' CONTRIBUTIONS

A.M.R. conceived the project, led the research planning, field work, data analysis and writing; S.K. contributed to project conceptual development, research planning and writing; A.S.G. contributed to conceptual development and writing; B.J.v.R. contributed to project conceptual development, analysis and writing. All the authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

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ORCID

Andrew M. Rogers https://orcid.org/0000-0002-3435-5040

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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