42 Competition and Invasive Species Impacts on Native Communities

Andrew M. Rogers* and Salit Kark

The Biodiversity Research Group, The School of Biological Sciences, Centre for Biodiversity and Conservation Science, The University of Queensland, Brisbane, QLD 4072 Australia

Citation: Rogers, A.M. and Kark, S. (2020) Competition and invasive species impact on native communities. In: Downs, C.T. and Hart, L.A. (eds) *Invasive Birds: Global Trends and Impacts*. CAB International, Wallingford, UK, pp. 340–348.

42.1 Introduction

Competition between birds can influence species' access to resources, altering species persistence within an environment and ultimately community structure. However, predicting where and when invasive species significantly compete with native species can be challenging due to a lack of information on interspecies interactions around resources in different environments. The extent to which critical resources, such as habitat space, territories, nesting sites and food, vary across different environments changes levels of competition and makes the importance of invasive–native species competition context specific. In order to better understand how competition between invasive and native species impacts invaded communities, it is important to identify critical resources, the species interacting over the resource and the functional traits that influence interaction frequency and outcome. Such an approach will allow a more mechanistic understanding of competition at the community level and facilitate better predictions of invasive bird impacts.

42.2 Competition as a Key Factor

Competitive interactions within bird communities can influence species access to resources and ultimately structure community composition at landscape scales (Minot and Perrins, 1986; Alatalo and Moreno, 1987; Montague-Drake *et al*., 2011; Farwell and Marzluff, 2013; Peck *et al*., 2014). In global assessments of invasive bird impacts, competition between invasive and native birds is generally considered to be of little ecological importance relative to other impacts such as predation and disease transmission (Blackburn *et al*., 2009). However, increasingly, studies have shown that invasive species can significantly impact native species through competitive interactions, especially when species are competing over resources critical to breeding such as nest sites and breeding territories (Ingold, 1998; Ghilain and Belisle, 2008; Brazill-Boast *et al*., 2010; Yosef *et al*., 2016). While invasive–native competition and aggression are often invoked as the mechanism driving patterns of reduced species richness or changes in breeding dynamics (e.g. nest site choice and breeding success), the mechanism of that competition is rarely quantified. Furthermore, much more work needs to be done on how competition is likely to vary in different landscapes or across different communities, as competitive interactions will often occur alongside other environmental changes, changing the relative importance of competitive impacts (Grarock *et al*. 2012).

Some of the best examples of significant competition in birds occur where species require the same critical resources (e.g. foraging space, breeding sites or territories) (Rusterholz, 1981; Remm *et al*., 2008; Menchetti and Mori, 2014; Sanz-Aguilar *et al*., 2015). However, identifying the form of the competitive impacts (e.g. direct aggression or more efficient resource exploitation; Griffin *et al*., 2012) for each member of an invaded community requires data on interspecies interactions among all species that require that resource. These interactions are often hard to observe, as they may occur infrequently or be habitat specific (e.g. for cavity-nesting species, interactions often occur high in tree canopies around tree hollows) (Davis, 2003; Kéfi *et al*., 2015). Novel use of technology and large spatial databases on species occurrence provide opportunities to explore competition and the patterns it creates in community structure. For example, Davis *et al*. (2013) used remote motion-activated camera traps to monitor birds and other species visiting nesting sites in tree hollows, demonstrating high levels of aggressive interactions around urban tree hollows and revealing the extent to which aggression is a driver of competition for a limited resource in woodland fragments in Sydney, Australia. At broader spatial scales, Cooper *et al*. (2007) found significant evidence of competition between introduced House Finches (*Haemorhous mexicanus*) and native House

*Corresponding author: a.munro.rogers@gmail.com

Sparrows (*Passer domesticus*) in the North American Christmas bird counts. As more landscape-scale databases on bird presence continue to grow with the aid of citizen science, more opportunities to explore individual species trends and test the importance of competition and its drivers at the species and community levels will be possible (Joyce *et al*., 2018).

Recent work has shown the importance of quantifying invasive species impacts on whole communities (Hui *et al*., 2016; Hui and Richardson, 2019). Where invasive–native interactions have been mapped at the community level, complex interaction graphical representations or webs have revealed both direct and indirect competitive interactions, with important implications for invasive species management (Orchan *et al*., 2013; Goldshtein *et al*., 2018). Describing the community-wide interaction network (where species are represented as nodes and connected by pairwise interactions or links between nodes; Fath *et al*., 2007) is critical for managing invaded communities to avoid perverse outcomes and optimally achieve efforts to mitigate invasive species impacts, especially in communities with multiple invasive species (Bode *et al*., 2015). For example, Orchan *et al*. (2013) found in the cavity breeding bird community (invaded by multiple invasive species) in a large urban park in Israel, that managing the invasive Common Myna (*Acridotheres tristis*) alone could lead to the competitive release of a second invasive species, the Venus-breasted Starling (*Acridotheres burmannicus*), which was more dominant over the native Syrian Woodpecker (*Dendrocopos syriacus*). In a study of interspecies fighting around bird feeders across North America, Miller *et al*. (2017) described the dominance hierarchy over food resources. This hierarchy revealed that, while the competitive dominance of species in general was predicted by larger body mass, some species were notable outliers that were more aggressively dominant than would be predicted by functional traits alone. In these studies, species interactions and functional traits were quantified at the community level and revealed more complex relationships between species than would have been found in studies of single species or species pairs.

In global assessments of invasive–native bird impacts, there is relatively little information on most invasive bird interactions with local species, and very few examples (relative to the number of introductions) of direct impacts of a species on native populations (Blackburn *et al*., 2009; Baker *et al*., 2014; Evans *et al*., 2016). Where impacts do occur, they are often the result of competition. Impacts from predation are considered more significant but are less common (Blackburn *et al*., 2009; Batalha *et al*., 2013). The lack of data on interspecies interactions is a limiting factor in assessing the global importance of invasive–native competition and hampers predictions of where significant impacts are likely to occur. Invasive species do not always significantly compete with native species where resources are not limited, or where there are differences in habitat preference (e.g. native species avoiding heavily modified environments that are often favoured by introduced species), or when a species can shift resources use (even slight differences in food preferences or foraging strategy, allowing species to reduce levels of competition) (Griffin *et al*., 2012; Batalha *et al*., 2013). Even where competitive impacts have been identified for an invasive species in one part of its invasive range, it is often hard to generalize these impacts across their global invasive range. For example, the Common or European Starling (*Sturnus vulgaris*) is invasive and widespread in both North America and Australia (among other regions), yet a lack of research focus on the drivers of competition in North America and a lack of interaction data in Australia make generalizations about its impacts globally uncertain. The impacts of this species across North America (mostly competition for nesting sites with other cavity-nesting species) varies significantly based on the local community and the habitat type invaded (Koenig, 2003; Linz *et al*., 2007). Similar variation is likely within and between continents, and more information on competitive interactions between starlings and native Australian bird species (as well as other cavity-dependent wildlife) from across its Australian range would provide a better context for understanding the potential impact across its global distribution.

Other factors that are likely to change interspecies interactions and therefore competitive impacts include invasive species abundance, environmental variation in resources, and the fluctuation in resource abundance or importance over time (Parker *et al*., 1999; Fogarty *et al*., 2011; Grarock *et al*., 2013; Simberloff *et al*., 2013). These factors are likely to be especially important for understanding when invasive impacts are likely, in turn allowing conservation managers to work in a more informed and targeted way rather than relying on the precautionary principle to justify management actions, such as invasive species control. Accounting for competitive interactions and the factors that influence them is especially important for the management of communities with multiple invasive species and where the impacts of management are uncertain (Bode *et al*., 2015; Baker *et al*., 2018). Therefore, in order to generate a more mechanistic understanding (incorporation of physiological ecology and ecomorphology into analysis of community ecology) (Schoener, 1986) of invasive bird competitive impacts, data must be collected on resource use, interacting species, the strength of those interactions, the functional traits related to resource use and the context in which the impacts occur. Such an approach will improve assessments of how invasive species change community-wide interactions and allow predictions of where and when invasive species are likely to significantly compete with native species (Dick *et al*., 2014).

42.3 A Framework for Assessing Species Interactions

To help include interactions into invasion studies and management for birds, we present a simple framework that outlines the steps required to map interactions and their drivers (Fig. 42.1). Such an approach will improve information on invasive species impacts on individual species as well as on communities (Rusterholz, 1981; Romanuk *et al*., 2009; Green *et al*., 2018), and will allow improved predictions of invasive species impacts beyond the immediate study area usually covered by invasive species studies. In particular, it is important to: (i) identify resources; (ii) identify the actors interacting around resources and the functional traits of those actors; (iii) identify all the relationships between interacting species; (iv) map the direction, strength and

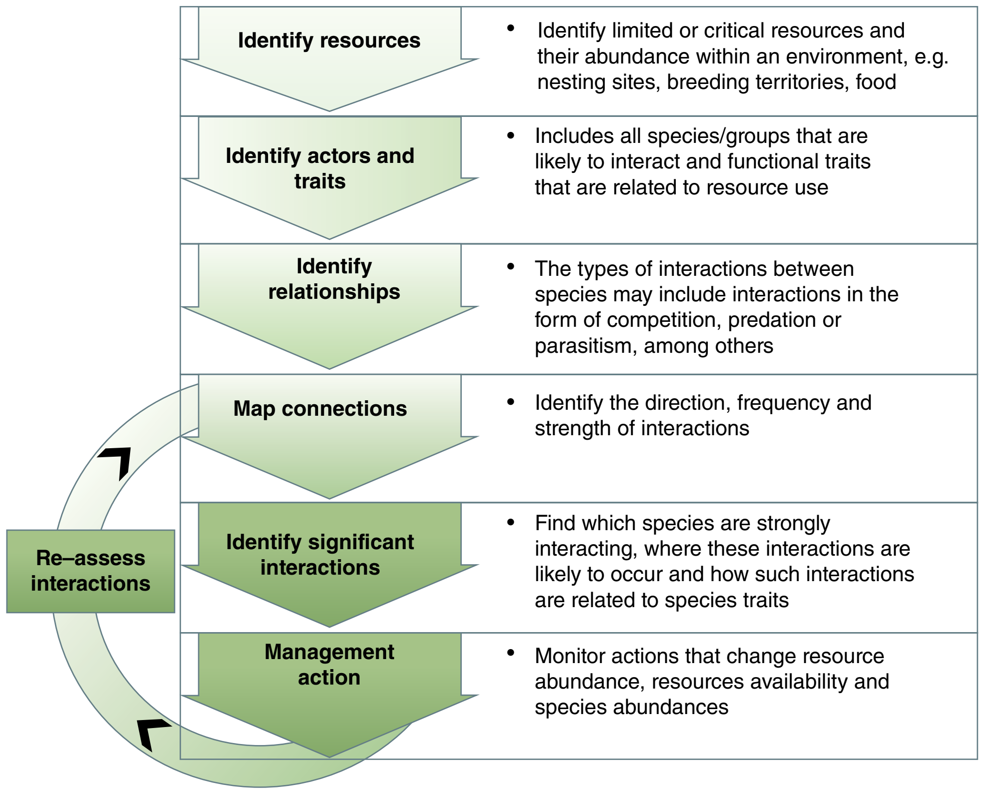

Fig. 42.1. By taking species interactions into account when evaluating the importance of competition, impacts on specific species can more easily be identified and targeted. This approach can reveal complex relationships at the community level that inform community dynamics and how species management should be undertaken.

frequency of the interactions, in multiple environmental contexts if possible; (v) identify the significant interactions within a given community; (vi) apply management actions; and finally (vii) reassess interactions between species to test how changes driven by management actions have altered species competitive relationships.

42.3.1 Identifying resources

Identifying critical resources such as nesting sites, breeding territories and foraging areas, around which species are likely to interact is one way to define a potentially interacting community (Dhondt, 2012). The habitat and environmental conditions in which the resources occur will provide important context, as variation in resource abundance and quality will change their importance for species (Le Roux *et al.*, 2016a). For example, in a study of nest box visitation by birds, Le Roux *et al.* (2016a) found that nest boxes on small trees were used at significantly lower rates compared with large trees, such that simply adding nest boxes to habitats is unlikely to increase nesting attempts by native birds. In similar studies for other nest box-using species, both the traits of the box and the surrounding habitats influenced whether the boxes were used by native species (Mänd *et al.*, 2005; Lindenmayer *et al.*, 2009; Le Roux *et al.*, 2016a,b).

42.3.2 Identifying the actors and traits

One of the primary challenges in assessing the importance of interactions in an invaded system is adequately surveying the species and their abundances within a community. Interactions should be more common between species that are more abundant, who co-occur, and who occupy more similar ecological niches. A species ecological niche includes its resource requirements and use, and can be influenced by the functional traits of the species. For example, the body size of cavity-nesting species reflects what size of nesting cavity they require, with larger species needing larger cavities in general. High overlap in the occupied niche space between species is often associated with high levels of competition (Rusterholz, 1981; Aderhold *et al.*, 2012; Green *et al.*, 2018; Reif *et al.*, 2018). Additionally, interacting species are likely to be a subset of the local species pool, creating challenges for identifying the limits of an interacting community, so efforts to quantify how completely a community has been sampled are important (Jordano, 2016).

42.3.3 Identify relationships

Species interacting around a resource will rarely, if ever, occur in isolation from the rest of the environment in which they occur. The presence of predators, parasites and other actors needs to be considered, as these can influence the risk associated with competing for a resource. Importantly, a single species may have multiple relationships with another one. For example, in cavity-nesting communities in Australia, cavity-using mammals both compete with birds for tree hollows and act as nest predators (Gibbons and Lindenmayer, 2002). Similarly, invasive birds such as the Common Myna have been known to destroy nests in some parts of its global range (Charter *et al.*, 2016), so understanding the conditions in which such nest predation occurs would be important when assessing the importance of competition for nest sites in tree hollows.

42.3.4 Map interactions between species

Mapping the interactions between species requires quantifying the interaction direction, frequency and variation in different environments. The direction of an interaction refers to the competitive impact of one species on another. For example, when fighting over food resources around bird feeders, direct aggressive interactions are observed between species pairs. For each interaction, the direction should be noted, where direction refers to the species that initiates or receives the interaction, or, if resource control is important, then the direction can reflect the species that most frequently wins the fight (i.e. the more dominant species).

42.3.5 Identify significant interactions

At this stage, it is important to test how species abundance, co-occurrence and interaction frequency within a specific context affect competition. The strength (frequency and intensity) of the interactions between two species can then be assessed relative to all the interactions among community members. Different interaction intensities can be quantified by the types of interactions; in the case of birds, physical fights could be considered a more intense interaction than alarm calls or threat displays. Interaction strength could also be quantified as how frequently one species is dominant over another, for example how many times a species disrupts the nesting attempts of another species (Edworthy, 2016) or how frequently a species excludes another species from a feeding resource (Peck *et al.*, 2014; Miller *et al.*, 2017). Both direct and indirect effects can be assessed at this point and used to inform management actions, such as which species or resource to prioritize or whether multi-species management will better mitigate invasive species impacts (Moon *et al.*, 2010; Bode *et al.*, 2015).

42.3.6 Manage the species

Activities that change resource abundance or availability, or alter species abundances, are likely to change competition over resources (Brazill-Boast *et al.*, 2013). Understanding the environmental or temporal contexts in which competitive impacts are the greatest between invasive and native species offers a more specific context in which to implement management actions. Furthermore, by incorporating the ecological niche of each species, slight differences in niche space can be exploited to reduce competition by excluding invasive species from accessing resources (Charter *et al.*, 2016; Goldshtein *et al.*, 2018).

42.3.7 Reassess interactions following management and changes in the system

When resources or species abundances have changed, interactions need to be reassessed. The strength of direct and indirect interactions will also change, with implications for follow-up management actions. After management, predictions on how interactions are likely to change (based on niche overlap, species abundance and resource use) with management can be tested by comparing levels of competition after management with pre-management conditions.

42.4 A Case Study for an Australian Cavity-dependent Species

Australia is home to some of the same invasive species that have been introduced in many other countries such as House Sparrows, Common Starlings and Common Mynas (see Chapter 36, this volume). Of these species, most research has focused on the Common Myna. The Common Myna has been shown to have significant impacts on native communities in other countries in which it is invasive, and the evidence of significant impacts on native Australian species varies depending on the habitat in which the myna occurs (although studies have only come from a small part of the invasive range in Australia). Competitive impacts of the Common Myna are especially interesting to explore in the Australian context because it is home to many cavity-nesting species, and cavities are limited resources in the modified habitats preferred by the Common Myna. Additionally, competition and aggression have a more significant role in structuring community composition in Australia compared with most places in the world.

Across the global invasive range of the Common Myna, impacts on native species include competition for habitat space, competition for nesting sites, and nest destruction and predation (see Chapter 3, this volume). Common Myna competition for habitat space has been invoked to explain declines in some bird species following the increases in myna abundance (Grarock *et al.* 2012) and increases in native bird abundance following myna eradication (Tindall *et al.*, 2007). In these studies, competition is often invoked to explain these patterns, but direct, aggressive interactions between mynas and native species are rarely quantified. When examining myna–native species competition for food in urban areas in Australia, Sol *et al.* (2012) and Haythorpe *et al.* (2014) found that Common Mynas were not more aggressive than native species around food resources, highlighting that the mechanism by which mynas impact other species use of foraging or habitat space is not well understood. Evidence of significant impacts on native species breeding is more substantial, such as aggressive interactions around nest sites and destruction of nests observed in Israel (Orchan *et al.*, 2013; Charter *et al.*, 2016) and from Pacific islands where the myna predates the nests of shorebirds (Byrd *et al.*, 1983). Despite significant impacts observed overseas, the evidence for significant impacts in Australia is mixed.

Like elsewhere, the most direct competitive impacts of the Common Myna in Australia come from studies of competition for nest sites, specifically when Common Mynas compete for nesting sites in less-disturbed habitats. In a study of nest site locations, Grarock *et al.* (2013) found that Common Mynas selected nest sites (in nest boxes) in more modified habitats, while native species selected nest sites in less modified habitats (areas with higher tree density), and concluded that the spatial segregation in nesting sites was a result of both habitat preferences and competition with Common Mynas. In a study of breeding success in nest boxes and tree hollows in open woodland, Pell and Tidemann (1997a) found that the Common Myna was the most aggressive cavity-nesting species compared to the invasive Common Starling and two native species. They concluded that this aggression could cause reduced breeding opportunities for the native species. While Common Mynas rarely nest deep into intact forests with high tree density (Pell and Tidemann, 1997b), impacts on nesting from competition are likely to be greatest where preferences for nest sites overlap. These areas include edge habitats (where urbanized and undisturbed environments meet), agricultural landscapes (particularly areas with a few large scattered trees) and native woodland with low tree density. Competition may become less important as levels of urbanization increase in areas characterized by suburban housing developments (where mynas can nest in buildings, under roofs and in rain gutters), as the effects of habitat change exclude native species more than competitive interactions.

Attempts to quantify the relative importance of additional competition from invasive species must also account for the high levels of aggression and competition among Australian native species (Sol *et al.*, 2012; Haythorpe *et al.*, 2014). Australian birds are known to be among some of the most aggressive birds globally (Low, 2014), with high levels of competition observed between species competing over foraging areas, breeding territories and nesting sites (Mac Nally and Timewell, 2005; Howes and Maron, 2009; Mac Nally *et al.*, 2012; Maron *et al.*, 2013). In particular, the native Noisy Miner (*Manorina melanocephala*) is a colony-nesting member of the honeyeater family, and so aggressively excludes other birds from its territories (in modified environments) that it is considered to impact bird communities at landscape scales (Montague-Drake *et al.*, 2011; Maron *et al.*, 2013). However, direct interactions responsible for these patterns are rarely quantified at the community level in Australia. The best examples of the importance of direct competitive interactions between species come from studies of cavity-nesting birds (Davis *et al.*, 2013), and include threatened native species such as the Forty-spotted Pardalote (*Pardalotus quadragintus*; Edworthy, 2016), Gouldian Finch (*Erythrura gouldiae*; Brazill-Boast *et al.*, 2010, 2013) and Palm Cockatoo (*Probosciger aterrimus*; Garnett *et al.*, 1999; Murphy *et al.*, 2003). Despite the importance of competition demonstrated for these species, and bird communities more generally, direct competitive interactions are not well understood for the cavity-nesting community at large, which includes 114 species of birds, and at least seven established invasive cavity-nesting species including the Common Myna.

In Australia, competition between Common Mynas and native bird species is likely to be greatest in moderately transformed environments; however, a lack of data on the relationship between functional traits (i.e. body size) and interspecific dominance prevents predictions of where the Common Myna will have an impact across its range. This, in turn, limits where managing the species would be most effective. While there are some efforts by local conservation groups to control the Common Myna through trapping, this approach is unlikely to reduce the population or reduce the impact of the Common Myna on native birds (see Chapter 3, this volume). Additionally, reducing Common Myna populations in urban areas may not improve nesting opportunities for native birds due to competition with other native urban-adapted species. In a study of urban cavity-nesting species in subtropical south-east Queensland, Rogers (2019) found a diverse community of cavity-dependent species using urban nest boxes, including the Common Myna (Fig. 42.2). While Common Mynas were found to be the most aggressive species around tree hollows, species recorded around nest boxes in the same region included several cavity-nesting birds, cavity-dependent mammals and other predators (Fig. 42.2). This work highlights that, even within the same region, interactions around different types of resources (tree hollows versus nest boxes) may be different. Additionally, the interactions between Common Mynas and native birds are occurring within a larger complex interaction web that includes predation and competition. In the case of common brushtail possums (*Trichosurus vulpecula*), this species is both a competitor for nest boxes and a nest predator of birds (Garnett *et al.*, 1999). While the interaction web described in Fig. 42.2 centres around nest boxes, similar processes are likely to be occurring around natural tree hollows but are poorly quantified. Nevertheless, like previous work, it appears that competitive interactions between Common Mynas and native species are context dependent. Competitive impacts are particularly high around natural tree hollows (Pell and Tidemann, 1997a), but native bird avoidance of nest boxes (perhaps due to interactions with native predators and native mammals) reduces the importance of competition around nest boxes.

Conservation efforts that aim to improve nesting opportunities for native cavity-nesting birds in Australia need to take into account all interactions among members of a community in order to identify which interactions may be limiting breeding opportunities (Heinsohn *et al.*, 2003; Murphy *et al.*, 2003; Brazill-Boast *et al.*, 2010; Stojanovic *et al.*, 2014). In the case of the Common Myna, competitive interactions will have a negative impact on native species in areas where Common Myna decide to nest in natural tree hollows or edge habitats. However, efforts to improve nesting opportunities for native species in modified environments in south-east Queensland through control of Common Myna populations alone are unlikely to generally succeed due to the high abundance of native competitors and predators. While nest boxes remain a popular conservation tool in Australia to increase the supply of available cavities, such projects are often of little use to species of conservation concern (Lindenmayer *et al.*, 2009, 2017). Incorporating a better

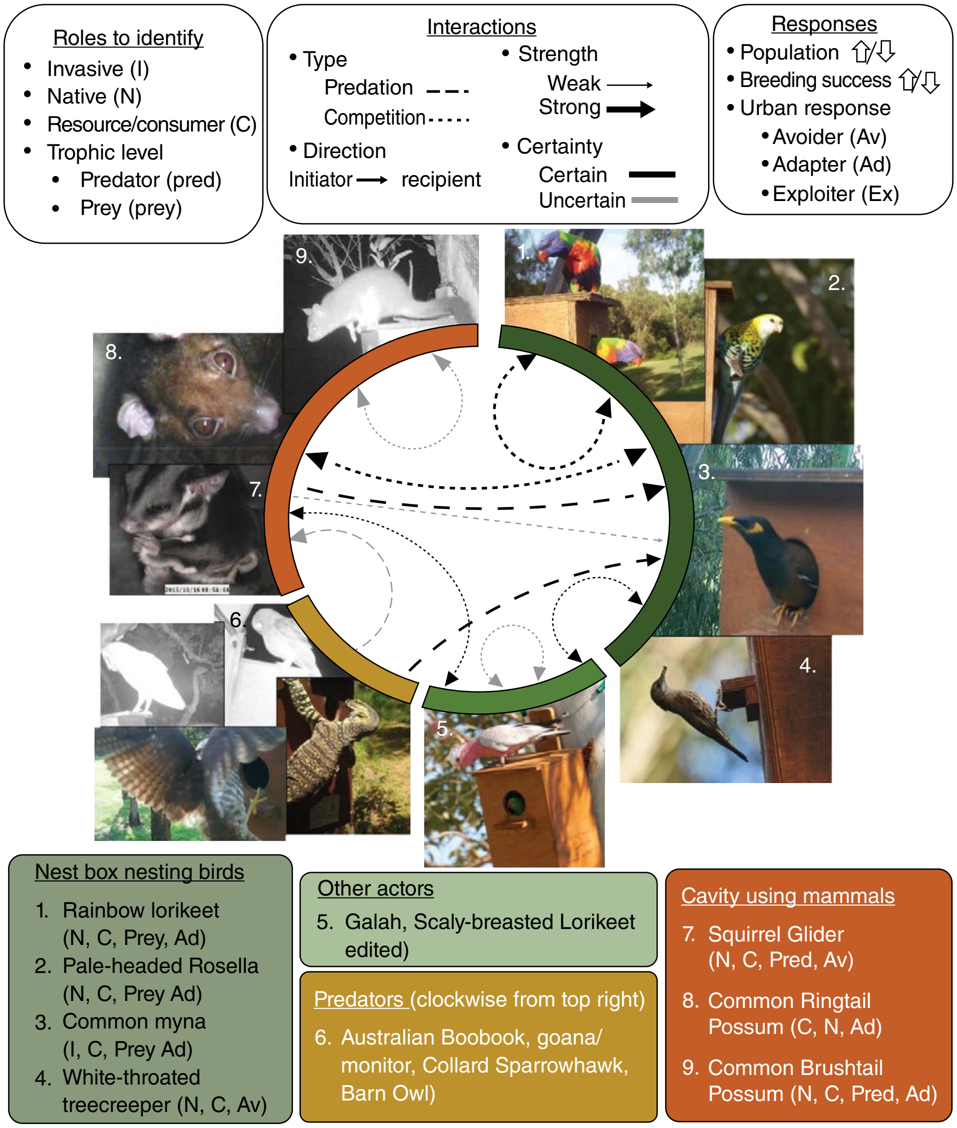

Fig. 42.2. The interaction web around nest boxes in south-east Queensland. Nest boxes were monitored with remote camera traps from October 2015 to March 2016, the peak breeding months in this region of Australia. The importance of invasive–native impacts needs to be assessed in the context of the community-wide interactions, including predation and competition among native species. The direction and strength of the interactions (arrows) between groups are essential for evaluating the importance of interactions such as competition. The response of an individual species to the total of the interactions within the network will influence its use and persistence within a habitat. In urban areas, these response groups include species that avoid urban areas (avoiders), species that adapt to use parts of urban environments (adapters) and species that can exploit urban environments (exploiters). (Photos: 1-4 & 6-9 A. Rogers; 5 Steve Gray).

understanding of interactions into such projects has been shown to increase their benefit to target species (Brazill-Boast *et al.*, 2013), and mapping all competitive and other interactions around different resources will improve management by identifying where and when invasive species interactions are most likely to impact breeding dynamics or use of habitat space.

The relative importance of invasive–native competition in the tangled interaction web around cavities in the urban environments of Australia is just starting to be quantified. The combined effects of habitat change, invasive species competition and changes in native species abundances none the less create challenges for conserving biodiversity in human-dominated environments (Kark *et al.*, 2007; Bellocq *et al.*, 2017). Species that are experts in exploiting urban areas are called ‘urban exploiters’, species that make some use of urban areas are called ‘urban adapters’ and species that avoid urban habitats are called ‘urban avoiders’ (Kark *et al.*, 2007; Shwartz *et al.*, 2008). Conservation efforts targeting urban adapters and avoiders within or at the edge of urban habitat fragments are likely to provide the greatest conservation benefit by increasing the resource availability in otherwise marginal habitats. In Fig. 42.2., the White-throated Treecreeper (*Cormobates leucophaea*) is an urban avoider that will use the same or similar nesting cavities as medium-sized parrots and the Common Myna in the same environment. Currently, relatively little is known about the exact nesting preferences of this treecreeper, which limits the ability of managers to exploit differences in nesting requirements and provide nest boxes that would exclude larger native or invasive birds. Nest boxes that are accessible to a wide variety of species are unlikely to be of much conservation benefit as they are frequently occupied by common species not in need of additional nesting opportunities (Lindenmayer *et al*., 2017). For the White-throated Treecreeper, and many other less abundant cavity-nesting birds in Australia, additional work is needed on specific nest box design and reducing competition in habitats dominated by urban exploiters.

While the Common Myna is perhaps the most studied invasive cavity-nesting species in Australia, seven other invasive cavity-nesting species are already established (Gibbons and Lindenmayer, 2002), and Australia is at high risk of additional non-native species establishing invasive populations (Vall-Ilosera and Cassey, 2017). Additionally, there are 21 native Australian species that have been moved or established outside their historic ranges (Gibbons and Lindenmayer, 2002). Like the patterns for invasive species globally, the interactions between non-native and native species are poorly studied and consequently little is known about how these introductions have altered local communities. Describing the competitive interaction networks for these communities has the potential to sustainably improve native species conservation by identifying management action that can reduce the competitive impact of invasive species in targeted ways (Orchan *et al*., 2013). Significant conservation opportunities exist in Australian cities (Garden *et al*., 2006; Ives *et al*., 2016), but understanding how species persist and coexist in urban areas will require more data on community-level interactions, especially as communities dynamically change in terms of ongoing environmental disturbance and novel species introductions (Mokross *et al*., 2014; Hui *et al*., 2016).

42.5 References

Aderhold, A., Husmeier, D., Lennon, J.J., Beale, C.M. and Smith, V.A. (2012) Hierarchical Bayesian models in ecology: Reconstructing species interaction networks from non-homogeneous species abundance data. *Ecological Informatics* 11, 55–64.

Alatalo, R.V. and Moreno, J. (1987) Body size, interspecific interactions and use of feeding sites in tits. *Ecology* 68, 1773–1777.

Baker, C.M., Holden, M.H., Plein, M., McCarthy, M.A. and Possingham, H.P. (2018) Informing network management using fuzzy cognitive maps. *Biological Conservation* 224, 122–128.

Baker, J., Harvey, K.J. and French, K. (2014) Threats from introduced birds to native birds. *Emu* 114, 1–12.

Batalha, H.R., Ramos, J.A. and Cardoso, G.C. (2013) A successful avian invasion occupies a marginal ecological niche. *Acta Oecologica* 49, 92–98.

Bellocq, M.I., Leveau, L.M. and Filloy, J. (2017) Urbanization and bird communities: spatial and temporal patterns. In: Murgui, E. and Hedblom, M. (eds) *Emerging from Southern South America. Ecology and Conservation of Birds in Urban Environments*. Springer International Publishing, Cham, Switzerland, pp. 35–54.

Blackburn, T.M., Lockwood, J.L. and Cassey, P. (2009) *Avian Invasions : The Ecology and Evolution of Exotic Birds*. Oxford University Press, Oxford.

Bode, M., Baker, C.M. and Plein, M. (2015) Eradicating down the food chain: optimal multispecies eradication schedules for a commonly encountered invaded island ecosystem. *Journal of Applied Ecology* 52, 571–579.

Brazill-Boast, J., Pryke, S.R. and Griffith, S.C. (2010) Nest-site utilisation and niche overlap in two sympatric, cavity-nesting finches. *Emu* 110, 170–177.

Brazill-Boast, J., Pryke, S.R. and Griffith, S.C. (2013) Provisioning habitat with custom-designed nest-boxes increases reproductive success in an endangered finch. *Austral Ecology* 38, 405–412.

Byrd, G.V., Moriarty, D.I. and Brady, B.G. (1983) Breeding biology of wedge-tailed shearwaters at Kilauea Point, Hawaii. *Condor* 85, 292.

Charter, M., Izhaki, I., Ben Mocha, Y. and Kark, S. (2016) Nest-site competition between invasive and native cavity nesting birds and its implication for conservation. *Journal of Environmental Management* 181, 129–134.

Cooper, C.B., Hochachka, W.M. and Dhondt, A.A. (2007) Contrasting natural experiments confirm competition between House Finches and House Sparrows. *Ecology* 88, 864–870.

Davis, A., Major, R.E. and Taylor, C.E. (2013) Housing shortages in urban regions: aggressive interactions at tree hollows in forest remnants. *PLoS One* 8, e59332.

Davis, M.A. (2003) Biotic globalization: does competition from introduced species threaten biodiversity? *Bioscience* 53, 481–489.

Dhondt, A.A. (2012) *Interspecific Competition in Birds*. Oxford University Press, Oxford.

Dick, J.T.A., Alexander, M.E., Jeschke, J.M., Ricciardi, A., MacIsaac, H.J., *et al*. (2014) Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. *Biological Invasions* 16, 735–753.

Edworthy, A.B. (2016) Competition and aggression for nest cavities between Striated Pardalotes and endangered Forty-spotted Pardalotes. *Condor* 118, 1–11.

Evans, T., Kumschick, S. and Blackburn, T.M. (2016) Application of the Environmental Impact Classification for Alien Taxa (EICAT) to a global assessment of alien bird impacts. *Diversity and Distributions* 22, 919–931.

Farwell, L.S. and Marzluff, J.M. (2013) A new bully on the block: does urbanization promote Bewick's wren (*Thryomanes bewickii*) aggressive exclusion of Pacific wrens (*Troglodytes pacificus*)? *Biological Conservation* 161, 128–141.

Fath, B.D., Scharler, U.M., Ulanowicz, R.E. and Hannon, B. (2007) Ecological network analysis: network construction. *Ecological Modelling* 208, 49–55.

Fogarty, S., Cote, J. and Sih, A. (2011) Social personality polymorphism and the spread of invasive species: a model. *American Naturalist* 177, 273–287.

Garden, J., McAlpine, C., Peterson, A., Jones, D. and Possingham, H. (2006) Review of the ecology of Australian urban fauna: a focus on spatially explicit processes. *Austral Ecology* 31, 126–148.

Garnett, S.T., Pedler, L.P. and Crowley, G.M. (1999) The breeding biology of the Glossy Black-Cockatoo *Calyptorhynchus lathami* on Kangaroo island, South Australia. *Emu* 99, 262–279.

Ghilain, A. and Belisle, M. (2008) Breeding success of tree swallows along a gradient of agricultural intensification. *Ecological Applications* 18, 1140–1154.

Gibbons, P. and Lindenmayer, D.B. (2002) *Tree Hollows and Wildlife Conservation in Australia*. CSIRO Publishing, Canberra.

Goldshtein, A., Markman, S., Leshem, Y., Puchinsky, M. and Charter, M. (2018) Nest-site interference competition with House Sparrows affects breeding success and parental care in Great Tits. *Journal of Ornithology* 159, 667–673.

Grarock, K., Tidemann, C.R., Wood, J. and Lindenmayer, D.B. (2012) Is it benign or is it a pariah? Empirical evidence for the impact of the common myna (*Acridotheres tristis*) on Australian birds. *PLoS One* 7, e40622.

Grarock, K., Lindenmayer, D.B., Wood, J.T. and Tidemann, C.R. (2013) Does human-induced habitat modification influence the impact of introduced species? A case study on cavity-nesting by the introduced common myna (*Acridotheres tristis*) and two Australian native parrots. *Environmental Management* 52, 958–970.

Green, D.S., Matthews, S.M., Swiers, R.C., Callas, R.L., Yaeger, J.S., *et al.* (2018) Dynamic occupancy modelling reveals a hierarchy of competition among fishers, grey foxes and ringtails. *Journal of Animal Ecology* 87, 813–824.

Griffin, A.S., Sol, D. and Bartomeus, I. (2012) The paradox of invasion in birds: competitive superiority or ecological opportunism? *Oecologia* 169, 553–564.

Haythorpe, K.M., Burke, D. and Sulikowski, D. (2014) The native versus alien dichotomy: relative impact of native noisy miners and introduced common mynas. *Biological Invasions* 16, 1659–1674.

Heinsohn, R., Murphy, S. and Legge, S. (2003) Overlap and competition for nest holes among eclectus parrots, palm cockatoos and sulphur-crested cockatoos. *Australian Journal of Zoology* 51, 81–94.

Howes, A.L. and Maron, M. (2009) Interspecific competition and conservation management of continuous subtropical woodlands. *Wildlife Research* 36, 617–626.

Hui, C. and Richardson, D.M. (2019) How to invade an ecological network. *Trends in Ecology and Evolution* 34, 121–131.

Hui, C., Richardson, D.M., Landi, P., Minoarivelo, H.O., Garnas, J. and Roy, H.E. (2016) Defining invasiveness and invasibility in ecological networks. *Biological Invasions* 18, 971–983.

Ingold, D.J. (1998) The influence of starlings on flicker reproduction when both naturally excavated cavities and artificial nest boxes are available. *Wilson Bulletin* 110, 218–225.

Ives, C.D. Lentini, P.E., Threlfall, C.G., Ikin, K., Shanahan, D.F., *et al.* (2016) Cities are hotspots for threatened species. *Global Ecology and Biogeography* 25, 117–126.

Jordano, P. (2016) Sampling networks of ecological interactions. *Functional Ecology* 30, 1883–1893.

Joyce, M., Barnes, M.D., Possingham, H.P. and van Rensburg, B.J. (2018) Understanding of avian assemblage change within anthropogenic environments using citizen science data. *Landscape and Urban Planning* 179, 81–89.

Kark, S., Iwaniuk, A., Schalimtzek, A. and Banker, E. (2007) Living in the city: can anyone become an 'urban exploiter'? *Journal of Biogeography* 34, 638–651.

Kéfi, S., Berlow, E.L., Wieters, E.A., Joppa, L.N., Wood, S.A., *et al.* (2015) Network structure beyond food webs: mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology* 96, 291–303.

Koenig, W.D. (2003) European starlings and their effect on native cavity-nesting birds. *Conservation Biology* 17, 1134–1140.

Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Bistricer, G., Manning, A.D. and Gibbons, P. (2016a) Enriching small trees with artificial nest boxes cannot mimic the value of large trees for hollow-nesting birds. *Restoration Ecology* 24, 252–258.

Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Bistricer, G., Manning, A.D. and Gibbons, P. (2016b) Effects of entrance size, tree size and landscape context on nest box occupancy: considerations for management and biodiversity offsets. *Forest Ecology and Management* 366, 135–142.

Lindenmayer, D.B., Crane, M., Evans, M.C, Maron, M., Gibbons, P., *et al.* (2017) The anatomy of a failed offset. *Biological Conservation* 210, 286–292.

Lindenmayer, D.B., Welsh, A., Donnelly, C., Crane, M., Michael, D., *et al.* (2009) Are nest boxes a viable alternative source of cavities for hollow-dependent animals? Long-term monitoring of nest box occupancy, pest use and attrition. *Biological Conservation* 142, 33–42.

Linz, G.M., Homan, H.J., Gaulker, S.M., Penry, L.B. and Bleier, W.J. (2007) European starlings: a review of an invasive species with far-reaching impacts. In: *Managing Vertebrate Invasive Species. USDA National Wildlife Research Center Symposium*, University of Nebraska – Lincoln, pp. 378–386. Available at: https://digitalcommons.unl.edu/nwrcinvasive/24 (accessed 12 November 2019).

Low, T. (2014) *Where Song Began: Australia's Birds and How They Changed the World*. Viking, Sydney, Australia.

Mac Nally, R. and Timewell, C.A.R. (2005) Resource availability controls bird-assemblage composition through interspecific aggression. *Auk* 122, 1097–1111.

Mac Nally, R., Bowen, M., Howes, A., McAlpine, C.A. and Maron, M. (2012) Despotic, high-impact species and the subcontinental scale control of avian assemblage structure. *Ecology* 93, 668–678.

Mänd, R., Tilgar, V., Lõhmus, A. and Leivits, A. (2005) Providing nest boxes for hole-nesting birds – does habitat matter? *Biodiversity and Conservation* 14, 1823–1840.

Maron, M., Grey, M.J., Catterall, C.P., Major, R.E., Oliver, D.L., *et al.* (2013) Avifaunal disarray due to a single despotic species. *Diversity and Distributions* 19, 1468–1479.

Menchetti, M. and Mori, E. (2014) Worldwide impact of alien parrots (Aves Psittaciformes) on native biodiversity and environment: a review. *Ethology, Ecology and Evolution* 26, 172–194.

Miller, E.T., Bonter, D.N., Eldermire, C., Freeman, B.G., Greig, E.I., *et al.* (2017) Fighting over food unites the birds of North America in a continental dominance hierarchy. *Behavioral Ecology* 28, 1454–1463.

Minot, E.O. and Perrins, C.M. (1986) Interspecific interference competition – nest sites for blue and great tits. *Journal of Animal Ecology* 33, 1–4.

Mokross, K., Ryder, T.B., Côrtes, M.C., Wolfe, J.D. and Stouffer, P.C. (2014) Decay of interspecific avian flock networks along a disturbance gradient in Amazonia. *Proceedings of the Royal Society of London B: Biological Sciences* 281, 20132599.

Montague-Drake, R.M., Lindenmayer, D.B., Cunningham, R.B. and Stein, J.A.A. (2011) Reverse keystone species affects the landscape distribution of woodland avifauna: a case study using the Noisy Miner (*Manorina melanocephala*) and other Australian birds. *Landscape Ecology* 26, 1383–1394.

Moon, D.C., Moon, J. and Keagy, A. (2010) Direct and indirect interactions. *Nature Education Knowledge* 3, 50.

Murphy, S., Legge, S. and Heinsohn, R. (2003) The breeding biology of palm cockatoos (*Probosciger aterrimus*): a case of a slow life history. *Journal of Zoology* 261, 327–339.

Orchan, Y., Chiron, F., Schwartz, A. and Kark, S. (2013) The complex interaction network among multiple invasive bird species in a cavity-nesting community. *Biological Invasions* 15, 429–445.

Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., *et al.* (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1, 3–19.

Peck, H.L., Pringle, H.E., Marshall, H.H., Owens, I.P.F. and Lord, A.M. (2014) Experimental evidence of impacts of an invasive parakeet on foraging behavior of native birds. *Behavioral Ecology* 25, 582–590.

Pell, A.S. and Tidemann, C.R. (1997a) The impact of two exotic hollow-nesting birds on two native parrots in savannah and woodland in eastern Australia. *Biological Conservation* 79, 145–153.

Pell, A.S. and Tidemann, C.R. (1997b) The ecology of the Common Myna in urban nature reserves in the Australian captial territory. *Emu* 97, 141–149.

Reif, J., Reifová, R., Skoracka, A. and Kuczyński, L. (2018) Competition-driven niche segregation on a landscape scale: Evidence for escaping from syntopy toward allotopy in two coexisting sibling passerine species. *Journal of Animal Ecology* 87, 774–789.

Remm, J., Lõhmus, A. and Rosenvald, R. (2008) Density and diversity of hole-nesting passerines: dependence on the characteristics of cavities. *Acta Ornithologica* 43, 83–91.

Rogers, A.M. (2019) The role of habitat variability and interactions around nesting cavities in shaping urban bird communities. PhD thesis, University of Queensland, Brisbane, Australia.

Romanuk, T.N., Zhou, Y., Brose, U., Berlow, E.L., Williams, R.J. and Martinez Neo, D. (2009) Predicting invasion success in complex ecological networks. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364, 1743–1754.

Rusterholz, K.A. (1981) Competition and the structure of an avian foraging guild. *American Naturalist* 118, 173–190.

Sanz-Aguilar, A., Carrete, M., Edelaar, P., Potti, J. and Tella, J.L. (2015) The empty temporal niche: breeding phenology differs between coexisting native and invasive birds. *Biological Invasions* 17, 3275–3288.

Schoener, T.W. (1986) Mechanistic approaches to community ecology: a new reductionism? *American Zoologist* 26, 81–106.

Shwartz, A., Shirley, S. and Kark, S. (2008) How do habitat variability and management regime shape the spatial heterogeneity of birds within a large Mediterranean urban park ? *Landscape and Urban Planning* 84, 219–229.

Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D.A., *et al*. (2013) Impacts of biological invasions: what's what and the way forward. *Trends in Ecology and Evolution* 28, 58–66.

Sol, D., Bartomeus, I. and Griffin, A.S. (2012) The paradox of invasion in birds: competitive superiority or ecological opportunism? *Oecologia* 169, 553–564.

Stojanovic, D., Koch, A.J., Webb, M., Cunningham, R., Roshier, D. and Heinsohn, R. (2014) Validation of a landscape-scale planning tool for cavity-dependent wildlife. *Austral Ecology* 39, 579–586.

Tindall, D.S., Ralph, J.C. and Clout, M.N. (2007) Changes in bird abundance following Common Myna control on a New Zealand island. *Pacific Conservation Biology* 13, 202–212.

Vall-Ilosera, M. and Cassey, P. (2017) Leaky doors: private captivity as a prominent source of bird introductions in Australia. *PLoS One* 12, e0172851.

Yosef, R., Zduniak, P. and Żmihorski, M. (2016) Invasive Ring-Necked Parakeet negatively affects indigenous Eurasian Hoopoe. *Annales Zoologici Fennici* 53, 281–287.