Are invasive species drivers of native species decline or passengers of habitat modification? A case study of the impact of the common myna (*Acridotheres tristis*) on Australian bird species

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Abstract Habitat modification and invasive species are significant drivers of biodiversity decline. However, distinguishing between the impacts of these two drivers on native species can be difficult. For example, habitat modification may reduce native species abundance, while an invasive species may take advantage of the new environment. This scenario has been described as the driver-passenger model, with 'passengers' taking advantage of habitat modification and 'drivers' causing native species decline. Therefore, research must incorporate both habitat modification and invasive species impact to successfully investigate native species decline. In this paper, we used the common myna (*Acridotheres tristis*) as a case study to investigate the driver-passenger model. We investigated changes in bird abundance, over 2 years, in relation to different habitat types and common myna abundance. We hypothesized that the common myna is both a passenger of habitat change and a driver of some bird species decline. Our results indicated that the abundance of many native species is greater in high tree density nature reserves, while the common myna was uncommon in these areas. Common myna abundance was almost three times higher in urban areas than nature reserves and declined rapidly as tree density in nature reserves increased. Our findings indicated that the common myna is primarily a passenger of habitat change. However, we also observed negative associations between common myna abundance and some bird species. We stress the importance of simultaneously investigating both invasive species impact and habitat modification. We suggest habitat restoration could be a useful tool for both native species recovery and invasive species control. Understanding the drivers of native species decline will help inform impact mitigation and direct further research.

Key words: driver-passenger model, Indian myna, introduced species, pest management, *Sturnus tristis*.

INTRODUCTION

Both habitat modification and the introduction of invasive species pose major threats to biodiversity across the globe (Sala *et al*. 2000; Davis 2003; Clavero & García-Berthou 2005; Pimentel *et al*. 2005; Westphal *et al*. 2008). Invasive species can often benefit from habitat modification (Farnsworth 2004; MacDougall & Turkington 2005; Didham *et al*. 2005b; Chace & Walsh 2006). However, the impact on native species can be a direct result of the invading species, or it can be compounded by habitat modification (Gurevitch & Padilla 2004; MacDougall & Turkington 2005; Didham *et al*. 2005b). As a result of

this complexity, it can be difficult to identify the true cause of native species decline (MacDougall & Turkington 2005; Didham *et al*. 2005b; Shine 2010).

Research often investigates the impact of human-induced habitat modification *or* the effects of invasive species on native species abundance (Fazey *et al*. 2005; Didham *et al*. 2005a). Studies that rely on correlations between native and invasive species abundance allow only weak inferences of impact to be made (Gurevitch & Padilla 2004). In fact, studies reliant on these correlations may mistakenly identify an invasive species as a driver of change (Gurevitch & Padilla 2004; Didham *et al*. 2005b). For example, in New England, the USA, native plant species decline was primarily driven by the same habitat variable that promoted invasive species; however, correlation did not imply causation (Farnsworth 2004). In this

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scenario, the invasive species were 'passengers' of habitat modification, not 'drivers' of native species decline (MacDougall & Turkington 2005; Didham *et al.* 2005b). Therefore, to successfully investigate native species decline, research must incorporate both habitat modification and invasive species impact (Parker *et al.* 1999; MacDougall & Turkington 2005; Didham *et al.* 2005b; Bradshaw *et al.* 2007; Davis *et al.* 2011).

In this paper, we used the introduced common myna (*Acridotheres tristis*) as an Australian case study to investigate the driver-passenger model. Specifically, we asked whether the common myna is a passenger of habitat modification or a driver of native species decline.

The common myna is listed as one of the world's worst invasive species (Lowe *et al.* 2000). There is concern that the common myna displaces native species through competitive domination of cavity-nest sites and territories (Pell & Tidemann 1997b; Harper *et al.* 2005; Dhami & Nagle 2009; Lowe *et al.* 2011). Despite this concern, there is only limited scientific evidence that demonstrates the impact of the common myna (Lowe *et al.* 2011). Some studies have found no evidence of common myna impact on native bird species (Wood 1996; Parsons *et al.* 2006; Lowe *et al.* 2011), while other research postulates that the common myna could drive native species decline (Pell & Tidemann 1997b; Dhami & Nagle 2009; Grarock *et al.* 2012). The species is described as being abundant in modified urban landscapes (Wood 1996; Pell & Tidemann 1997a; Parsons *et al.* 2003; White *et al.* 2005; Peacock *et al.* 2007; van Rensburg *et al.* 2009; Lowe *et al.* 2011), but tends to avoid high density native woodland areas (Pell & Tidemann 1997a; White *et al.* 2005; Crisp & Lill 2006; Tracey *et al.* 2007; Lowe *et al.* 2011).

We investigated changes in bird abundance, over 2.5 years, in relation to different habitat types and common myna abundance. Our study was not as robust as controlled removal and long-term before and after experiments (Newton 1998; Blossey 1999; Ricciardi *et al.* 2000; Lindenmayer *et al.* 2005). However, we used present day variations in habitat and invasive species abundance to infer the effects of long-term changes on native species abundance. By including environmental variables in our analysis, we aimed to identify whether the common myna was a driver of native species decline or a passenger of habitat modification.

To investigate the passenger-driver model for the common myna, we developed and tested three hypotheses:
1. The common myna would be more abundant in urban habitats than in nature reserves.
2. Common myna abundance would increase as tree density declined.

3. Common myna abundance would have a negative impact on the abundance of some cavity-nesting species and small bird species.

Understanding the drivers of native species decline will help direct further research and better inform managers to conduct impact mitigation (MacDougall & Turkington 2005; Didham *et al.* 2005b). For example, invasive species management may not assist threatened species recovery if habitat quality is the major cause of species decline (Didham *et al.* 2005b).

METHODS

Survey sites

To investigate our hypotheses, we selected survey sites in the city of Canberra, Australia (Fig. 1). Each site was located in a suburban subdivision adjacent to a nature reserve. Sites were restricted to subdivisions greater than 20 years old and were situated at least 2 km apart. These criteria limited the potential study sites to 23. We estimated tree density in the 23 nature reserves by walking a 1-km transect scoring the vegetation cover at 20-m intervals. We allocated one point for tree cover overhead or zero points for no tree cover.

In order to select 15 survey sites, we chose the five sites with the highest vegetation score (>40), the five sites with a medium vegetation score (between 31 and 36) and the five sites with the lowest vegetation score (≤26) (Fig. 2a). We used an analysis of variance (ANOVA) to test if mean nature reserve tree density varied significantly among the three categories (high, medium and low) (Fig. 2b). Using a Geographic Information System (GIS) layer of native street trees in urban areas, we observed that tree density fell into the same high, medium and low categories as the adjoining nature reserves. We confirmed this using an ANOVA (Fig. 2c). As a result of this finding, we broadly defined each site (consisting of both urban and nature reserve area) as having either high, medium or low tree density.

Bird surveys

At each site we established two transect surveys. The first transect ran through the nature reserve and the second, at a right-angle to the first, through the urban area (suburb) (Fig. 1). Transects were 1 km in length, 100 m wide in the nature reserves and 60 m wide in the urban areas. Within each site, we expected that the habitat surrounding one transect may influence the abundance and diversity of birds in the other transect because of their close proximity (1 km^2) (Chapman & Reich 2007; Palomino & Carrascal 2007). Therefore, paired transects (in urban and nature reserves) were treated as a single site, with 15 sites in total.

We surveyed our 15 sites every second month (January, March, May, July, September, November) from September 2008 to March 2011. Experienced bird observers identified birds by both sight and call, using line transect surveys. We assigned each observer to a group of three sites (six transects)
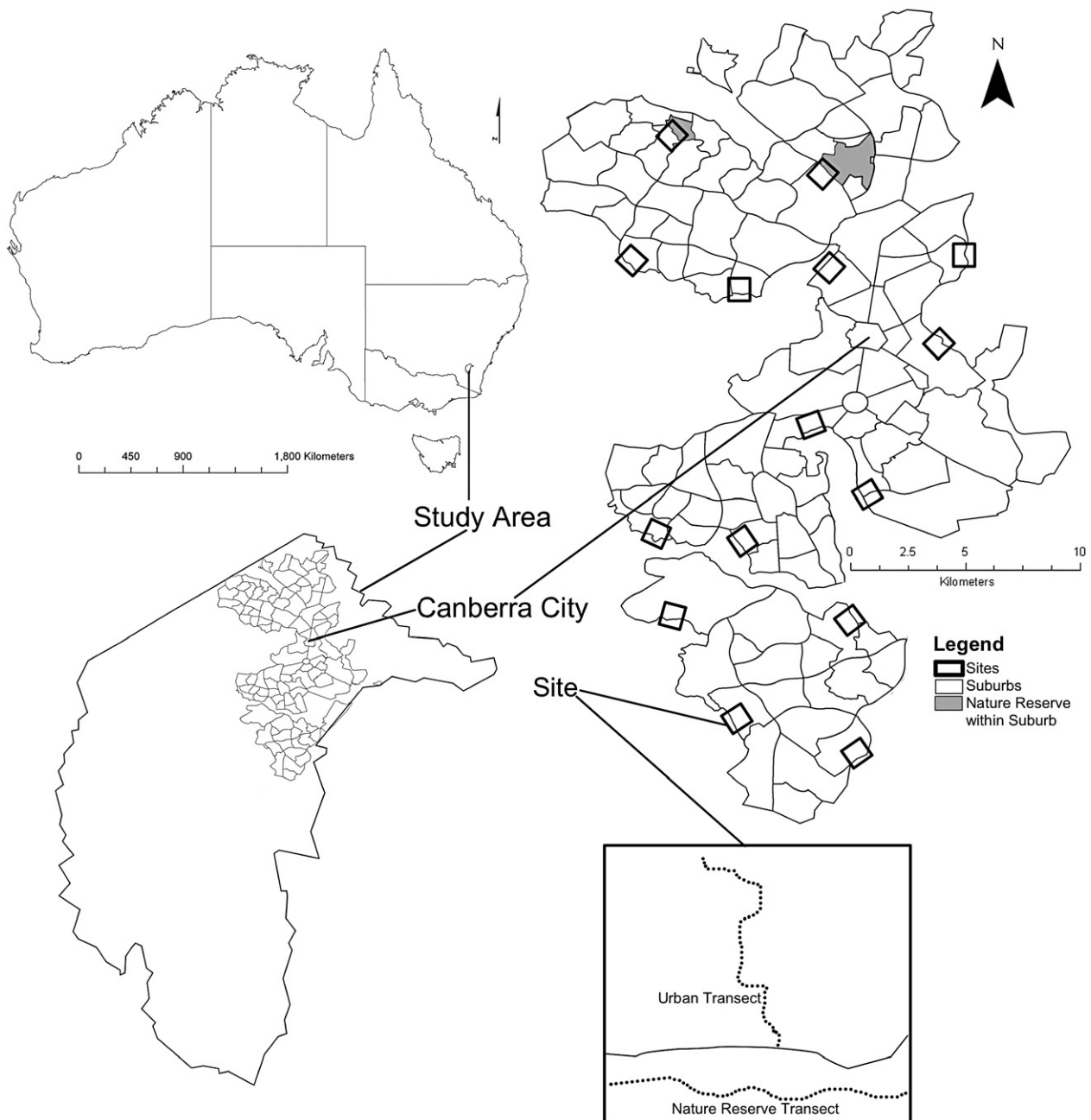
Fig. 1.   Study area and location of the 15 survey sites in Canberra, South East Australia. Sites were located in a suburb greater than 20 years old and adjacent to a nature reserve. At each site we set up two, 1-km, line transect surveys. Transects were 1 km in length, 100 m wide in the nature reserves and 60 m wide in the urban areas.

to survey. Observers walked transects for 20 min, within 3 h of sunrise. We ensured surveys were undertaken in good weather conditions with little or no rain or wind. Fifteen observers completed a total of 1071 transect surveys. Each transect was walked two or three times per survey month.

Preliminary data analysis

Earlier research indicated that the common myna may affect cavity-nesting species and small bird species, but not large

bird species (Pell & Tidemann 1997b; Harper *et al*. 2005; Tindall *et al*. 2007; Dhami & Nagle 2009; Grarock *et al*. 2012). We defined cavity-nesting species to be those that primarily nested in cavities and had a mean body weight greater than 3.03 g. Species lighter than 3.03 g (2 g less than the common myna) could potentially occupy cavities that were too small for the common myna. Small species were defined as having a mean body weight of 0.5 g less than the common myna. To conduct the analysis, we selected the 40 most abundant bird species within the following categories: 10 cavity-nesting species (>3.03 g), 20 small bird

(a)

High Tree Density   Medium Tree Density   Low Tree Density

(b)

(c)
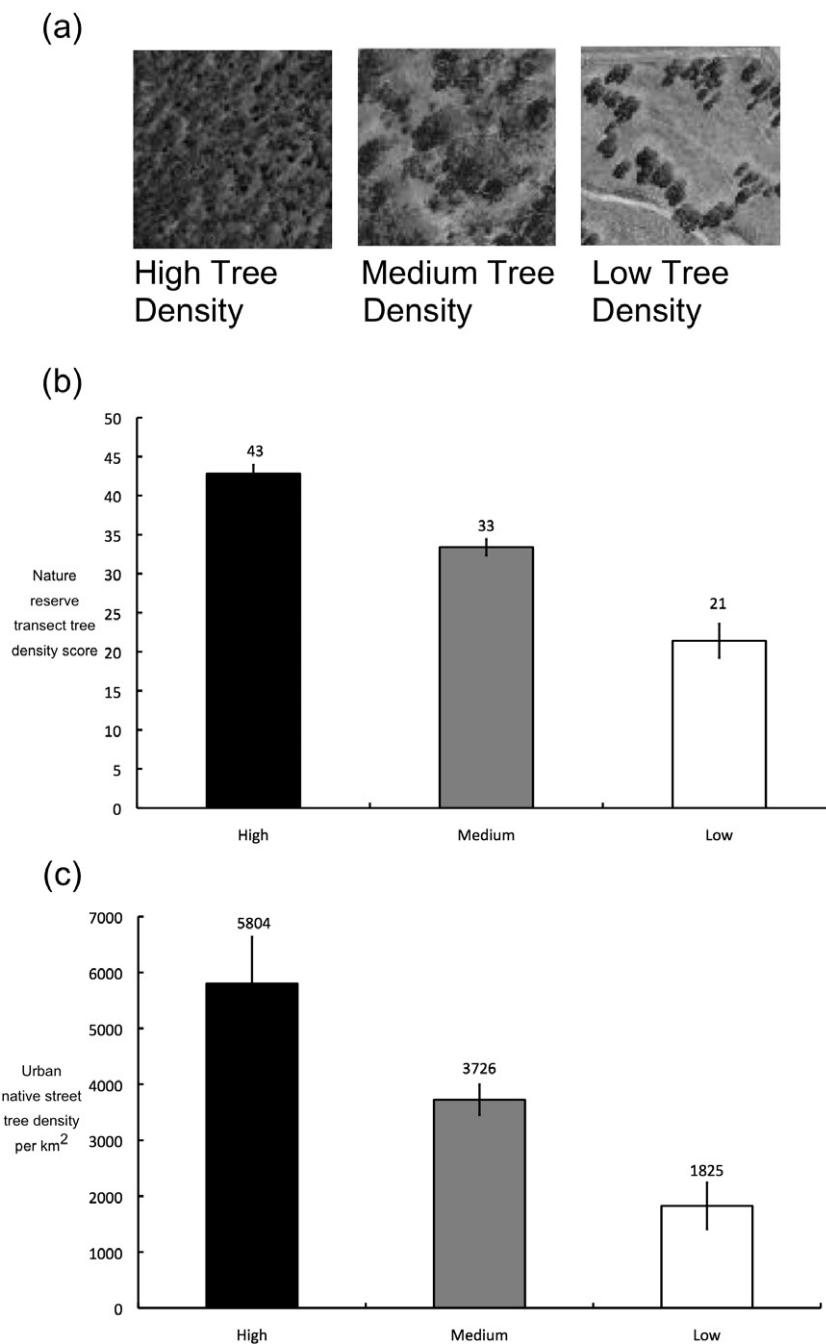
Fig. 2. Tree density of the 15 sites across Canberra, South East Australia. (a) Examples of the high, medium and low tree densities categories in nature reserves. (b) Graph of transect mean tree density score ($\pm$ SE) of nature reserve across the three tree density categories. (c) Graph of the mean tree density per square kilometre ($\pm$ SE) of urban areas across the three tree density categories. Tree density in suburbs ($F_{2,12} = 22.0$, $P < 0.001$) and nature reserves ($F_{2,12} = 12.5$, $P = 0.001$) was significantly different between the high-, medium- and low-tree-density sites.

species (≤ 4.53g) and 10 large bird species (>4.53 g) (Appendixes S1 and S2). Three of the small bird species can use cavities for nesting; however, their small size (<2.85 g) may limit cavity-nesting competition (Appendix S1). The 10 large bird species were not cavity-nesting species. We provide a list of the 40 target species analysed in Appendix S2. We also selected the following variables for

analysis: total species abundance and richness, native cavity-nester bird abundance and richness, small native bird abundance and richness, and large native bird abundance and richness. The common myna was not included in any of the above species groupings.

For each transect, we calculated the average number of birds observed per square kilometre (for every species) over

the replicated surveys in a month. This reduced the large number of zero values in the data. We then applied a $\log(x + 1)$ transformation to ensure data were approximately normally distributed.

To check that bird detection rates were similar for both reserve and suburb transects, we assumed that the transect surveys for a season (breeding or non-breeding season) could be treated as replicates. We estimated detection rates for each transect type, for selected species, from binomial mixtures models (Kery *et al.* 2005) using the R package unmarked (Fiske & Chandler 2011). Unfortunately, the low abundance of many species prevented us from performing meaningful detectability analysis. Therefore, we performed detectability analysis on the six most abundant species. These species were the common myna, magpie lark (*Grallina cyanoleuca*), crimson rosella (*Platycercus elegans*), spotted pardalote (*Pardalotus punctatus*), Australian magpie (*Gymnorhina tibicen*) and brown thornbill (*Acanthiza pusilla*).

Autoregressive model analysis

We fitted mixed models in GenStat 14 (VSN International 2011) using restricted maximum likelihood to investigate the factors that influenced: (i) common myna abundance; (ii) the abundance of the 40 target species; and (iii) the abundance and richness of particular species groupings. We included the following explanatory variables in the model: area (urban or nature reserve), tree density (high, medium and low), urban housing density per km^2, season (breeding: November to March and non-breeding: May to September) and year (1, 2 and 3). We also included common myna abundance as an explanatory variable for all analyses except for those exploring abundance of the common myna itself. We treated site as a random effect and used Wald tests for dropping individual terms from the full fixed model, until only significant (<0.05) explanatory variables remained.

We used the table of effects from the GenStat 14 (VSN International 2011) output, to observe the *influence* (either positive >0.00 or negative <0.00) each significant variable had on species abundance or species richness. We also used the table of predicted means, from the model output, to estimate (reverse $\log(x + 1)$ transformed) species abundance across different areas.

The breeding season for many species in Canberra starts later than in other areas of Australia because of the altitude (605 m above sea level) and colder weather (Lenz 1979; Gibbs *et al.* 2011). Therefore, we defined the breeding season as beginning in October and ending in March. We sourced data on house density from the Australian Bureau of Statistics (ABS 2006).

RESULTS

Detection rates

The estimated detection rates in the nature reserve transect (100 m wide) and the urban transect (60 m wide) were not significantly different for four of the six

species we analysed (common myna, magpie lark, spotted pardalote and brown thornbill). Detectability bias may occur for the crimson rosella, Australian magpie and other species not analysed. Therefore, results for these species should be treated with some caution. However, we believe bird survey estimates represent a constant proportion of the actual population present. Our study did not attempt to quantify the exact number of individuals present at each site, rather we examined the general influence of habitat and the common myna on bird abundance.

Common myna response to habitat variation

We found significant relationships between the abundance of the common myna and urban area, tree density, season and year (Table 1). The reverse $\log(x + 1)$ transformed predicted means (derived from the model in Table 1), indicated that common myna abundance in nature reserves was 13.6 birds per square kilometre, while in urban areas it was almost three times higher at 41.1 birds per square kilometre. This finding supported our hypothesis that the common myna would be more abundant in urban habitats than in nature reserves.

We also identified a significant negative relationship between common myna abundance and tree density in nature reserves ($F_{2,14} = 23.4, P < 0.001$). The predicted means, derived from the model in Table 1, indicated that common myna abundance in low tree density nature reserves was 44.2 birds per square kilometre, 18.5 birds per square kilometre for medium tree density and 2.5 birds per square kilometre for high tree density nature reserves. This finding supported our hypothesis that common myna abundance would increase as tree density declines.

Tree density in urban areas also influenced common myna abundance. The predicted means, derived from the model in Table 1, indicated that high tree density urban areas had lower common myna numbers (27.8 birds per square kilometre) than in medium (55.5 birds per square kilometre) and low (44.7 birds per square kilometre) tree density areas. Therefore, the common myna was strongly influenced by habitat and appeared to be a passenger of habitat change.

Species abundance and richness

Total species abundance was positively associated with high tree density areas ($F_{2,19} = 39.5, P < 0.001$), the non-breeding season ($F_{1,130} = 15.9, P < 0.001$), later years ($F_{2,129} = 9.7, P < 0.001$) and abundance of the common myna ($F_{1,140} = 8.7, P = 0.004$). We found no significant relationship between common myna abundance and total species richness (Table 1).

Table 1. Significant explanatory variables for restricted maximum likelihood analysis of common myna (*Acridotheres tristis*) abundance and species groupings in Canberra, South East Australia

Species/species group	Area Nature to urban	Tree density Nature High to medium	Nature High to low	Urban High to medium	Urban High to low	Human housing density (km²)	Season Breeding to non-breeding	Year Year 1 to year 2	Year 1 to year 3	Common myna abundance
Common myna (*Acridotheres tristis*)	0.91 ± 0.10 $P < 0.001$	0.74 ± 0.24 $P < 0.001$	1.11 ± 0.24 $P < 0.001$	0.29 ± 0.24 $P < 0.001$	0.20 ± 0.24 $P < 0.001$		−0.24 ± 0.07 $P = 0.002$	−0.15 ± 0.08 $P = 0.013$	−0.23 ± 0.08 $P = 0.013$	N/A
Total species abundance		−0.05 ± 0.06 $P < 0.001$	−0.12 ± 0.06 $P < 0.001$	−0.06 ± 0.06 $P < 0.001$	−0.16 ± 0.06 $P < 0.001$		0.08 ± 0.02 $P < 0.001$	0.07 ± 0.02 $P < 0.001$	0.09 ± 0.02 $P < 0.001$	0.07 ± 0.02 $P = 0.004$
Total species richness	0.01 ± 0.02 $P = 0.003$	0.06 ± 0.03 $P = 0.018$	−0.03 ± 0.03 $P = 0.018$	0.01 ± 0.03 $P = 0.018$	−0.07 ± 0.03 $P = 0.018$	−0.0003 ± 0.0001 $P = 0.020$	−0.02 ± 0.01 $P = 0.002$	0.03 ± 0.01 $P = 0.003$	0.03 ± 0.01 $P = 0.003$	
Native cavity-nester bird abundance	0.12 ± 0.03 $P < 0.001$						0.15 ± 0.03 $P < 0.001$			
Native cavity-nester bird richness	−0.04 ± 0.02 $P < 0.001$	−0.01 ± 0.04 $P = 0.037$	−0.13 ± 0.04 $P = 0.037$	−0.03 ± 0.04 $P = 0.037$	−0.13 ± 0.04 $P = 0.037$		0.03 ± 0.01 $P = 0.007$			
Small native bird abundance*		0.09 ± 0.01 $P = 0.002$	−0.08 ± 0.01 $P = 0.002$	−0.04 ± 0.01 $P = 0.002$	−0.23 ± 0.01 $P = 0.002$	−0.001 ± 0.0004 $P = 0.029$				−0.08 ± 0.04 $P = 0.035$
Small natives richness*	−0.04 ± 0.02 $P < 0.001$						−0.03 ± 0.02 $P = 0.049$	0.05 ± 0.02 $P = 0.003$	0.05 ± 0.02 $P = 0.003$	−0.06 ± 0.02 $P < 0.001$
Large native bird abundance	0.20 ± 0.02 $P < 0.001$						0.11 ± 0.02 $P < 0.001$	0.07 ± 0.02 $P < 0.001$	0.08 ± 0.02 $P < 0.001$	0.09 ± 0.02 $P < 0.001$
Large native bird richness	−0.05 ± 0.01 $P < 0.001$						−0.03 ± 0.01 $P = 0.002$	−0.01 ± 0.01 $P = 0.028$	−0.03 ± 0.01 $P = 0.028$	

Analysis initially included all explanatory variables in the model and then we sequentially removed non-significant variables until only significant (<0.05) variables remained. Values in the table indicate the *effect* (either positive >0.00 or negative <0.00) each variable had on log(x + 1) transformed species abundance or species richness (± SE). For example, the positive value of 0.91 indicates that common myna abundance was greater in urban areas than in nature reserves. Nature reserve is given a zero value and the effect of urban areas relative to nature reserve is reported. Likewise, tree density is reported as a deviation from high tree density to either medium or low tree density, season is reported as a deviation from breeding season to non-breeding season and year is reported as a deviation from year 1 to either year 2 or year 3. The values reported for human housing density and the common myna give the coefficients of these variables. An asterisk (*) indicates species groupings that were negatively associated with common myna abundance.

Cavity-nesting species

We did not identify any significant relationships between common myna abundance and native cavity-nesting species abundance or richness (Table 1). Native cavity-nester abundance was positively associated with urban areas ($F_{1,133} = 21.1$, $P < 0.001$) and the non-breeding season ($F_{1,133} = 29.5$, $P < 0.001$). Native cavity-nester richness was positively associated with nature reserve areas ($F_{1,131} = 22.9$, $P < 0.001$), high tree density areas ($F_{2,14} = 5.8$, $P = 0.037$) and the non-breeding season ($F_{1,131} = 7.4$, $P = 0.007$) (Table 1).

We found a negative relationship between the abundance of the common myna and the abundance of the gang-gang cockatoo (*Callocephalon fimbriatum*) ($F_{1,145} = 11.8$, $P < 0.001$) and crimson rosella ($F_{1,145} = 4.5$, $P = 0.036$) (Appendix S2). These findings supported our hypothesis that the common myna would negatively affect the abundance of some cavity-nesting species and, therefore, potentially drive the decline of these species.

We observed significant positive relationships between common myna abundance and three cavity-nesting species: the eastern rosella (*Platycercus eximius*) ($F_{1,646} = 10.5$, $P = 0.001$), red-rumped parrot (*Psephotus haematonotus*) ($F_{1,108} = 7.6$, $P = 0.007$) and common starling (*Sturnus vulgaris*) ($F_{1,122} = 19.1$, $P < 0.001$). No significant relationships were observed between common myna abundance and little

corolla (*Cacatua sanguinea*), sulphur-crested cockatoo (*Cacatua galerita*), Australian king-parrot (*Alisterus scapularis*) or laughing kookaburra (*Dacelo novaeguineae*) abundance (Appendix S2).

Small bird species

Our research identified significant negative relationships between common myna abundance and small native species abundance ($F_{1,141} = 4.5$, $P = 0.035$) and small native bird species richness ($F_{1,143} = 21.3$, $P < 0.001$) (Table 1). This supported our hypothesis that the common myna would negatively affect the abundance of some small bird species. We observed a significant positive relationship between nature reserve areas and small native species richness ($F_{1,134} = 30.4$, $P < 0.001$) (Table 1). Urban areas with high tree density supported a greater abundance of small native species than urban areas with medium or low tree density (Table 1).

We identified significant negative relationships between common myna abundance and the abundance of eight of the 20 small bird species we examined (Appendix S2). These eight species were: white-throated treecreeper (*Cormobates leucophaea*), spotted pardalote, speckled warbler (*Pyrrholaemus saggitatus*), brown thornbill, buff-rumped thornbill (*Acanthiza reguloides*), eastern spinebill (*Acanthorhynchus tenuirostris*), grey fantail (*Rhipidura*

fuliginosa) and grey butcher bird (*Cracticus torquatus*). The brown thornbill, buff-rumped thornbill and grey fantail were significantly more likely to be found in nature reserves than in urban areas (Appendix S2). These findings supported our hypothesis that the common myna would negatively affect the abundance of some small bird species and therefore, potentially drive the decline of these species.

Large bird species

We found a significant positive relationship between large native bird abundance and common myna abundance ($F_{1,144} = 11.6$, $P < 0.001$). We did not identify a significant relationship between common myna abundance and large native bird species richness (Table 1). Large native bird abundance was significantly higher in urban areas ($F_{1,135} = 195.0$, $P < 0.001$), while large native bird species richness was significantly lower in these areas ($F_{1,131} = 40.6$, $P < 0.001$) (Table 1).

No negative relationships between common myna abundance and the abundance of any of the 10 large bird species were observed (Appendix S2).

DISCUSSION

Our investigation of the common myna in Canberra provided a valuable case study to test the driver-passenger model. We used linear models to investigate changes in bird abundance and make inferences about the different drivers of native species decline. The key findings of our study were:
1. The common myna appeared to be primarily a passenger of habitat change.
2. In combination with habitat change, the common myna also appeared to be a driver of some bird species decline.
3. It is essential to simultaneously investigate invasive species impact and habitat modification to assist with differentiating between the impacts on native species.

The common myna was strongly influenced by tree density and showed a preference for urban areas. We did not find negative associations between common myna abundance and total species abundance and richness, native cavity-nester abundance and richness or large native bird abundance and richness. These results are consistent with the conclusions of Lowe *et al.* (2011) and Parsons *et al.* (2003) that the common myna is a passenger of habitat modification. However, unlike these earlier studies, we did find that small native species abundance and richness and some individual cavity-nesting species and small bird species, were negatively associated with the abundance of the common myna. This indicates that the common

myna may also drive the decline of *some* bird species. This finding is supported by our previous research (Grarock *et al.* 2012) that investigated the long-term abundance of bird species, before and after common myna invasion of Canberra, Australia.

Clearly not all causal variables have been included in our model with some unexpected results observed. For example, common myna abundance had a positive association with eastern rosella abundance. There may be a complex relationship between reductions in other cavity-nesting species (e.g. the crimson rosella) and increases in eastern rosella abundance. We also did not attempt to include the influence of other species such as the noisy miner (*Manorina melanocephala*) or the domestic cat (*Felis catus*) on native bird species abundance. The patterns observed in our study (limited to 15 sites in Canberra) may differ from those in other bioregions and in areas experiencing different stages of common myna invasion.

We suggest tree density is the key difference between our study and other investigations that found no negative correlations between common myna abundance and native species (Parsons *et al.* 2003; Lowe *et al.* 2011). Our study encompassed low-, medium- and high-tree-density sites, while Lowe *et al.* (2011) described their study site as having high tree density.

Low tree density in nature reserves, or fragmentation of native vegetation, may enhance habitat quality for the common myna enabling the species to spread into new areas and compete for resources with native species (Tracey *et al.* 2007; Lowe *et al.* 2011). Low-tree-density sites are probably similar to the natural environment of the common myna in India and central and southern Asia (Pell & Tidemann 1997a; Feare & Craig 1998).

We observed that the abundance of many native species was greater in nature reserves than in urban areas, and that abundance increased further with higher tree density. We also observed that the common myna was uncommon in high tree density nature reserves. Common myna abundance was almost three times higher in urban areas than nature reserves and declined rapidly as tree density in nature reserves increased. This observation is supported by studies that documented high densities of the common myna in disturbed and urban habitats (Pell & Tidemann 1997a; Feare & Craig 1998; Parsons *et al.* 2003; White *et al.* 2005; Crisp & Lill 2006; Dhami & Nagle 2009; Perry *et al.* 2009; van Rensburg *et al.* 2009; Lowe *et al.* 2011). Other studies have also reported increased native species abundance in response to greater native tree density (Clergeau *et al.* 1998; Sewell & Catteral 1998; Blair 2001; Crooks *et al.* 2004; Munro *et al.* 2009; Gardali & Holmes 2011).

The results of our study suggest that the effects of habitat modification and invasive species are interrelated. Many species are strongly influenced

by habitat, with greater abundance in high-quality habitat than in low-quality habitat (Kajzer *et al.* 2011). However, high-quality habitat for one species may not constitute high-quality habitat for another species (Farnsworth 2004; MacDougall & Turkington 2005; Didham *et al.* 2005b). Our results indicated that both human habitat modification and the common myna had negative impacts on some bird species. Therefore, in combination, habitat modification and the introduction of invasive species could have a substantial impact on native taxa (Gibbons & Lindenmayer 2002; Lindenmayer *et al.* 2009).

Given the influence of habitat on species abundance, we suggest that habitat restoration and tree planting may be useful tools to both control common myna abundance and aid native bird species recovery. Other Australian studies have suggested vegetation regeneration and dense planting of vegetation in reserves could be used as a method to control bird species such as the noisy miner and the bell miner (*Manorina melanophrys*) (Clarke & Schedvin 1999; Kemmerer *et al.* 2008; Taylor *et al.* 2008; Lindenmayer *et al.* 2010; Montague-Drake *et al.* 2011).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. List of species observed.
Appendix S2. Significant explanatory variables for restricted maximum likelihood analysis.