

RESEARCH ARTICLE

Bird community recovery following removal of an invasive tree

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Abstract

1. Faunal responses to plant invasions and their managed removal can expand our understanding of the nature of disturbance and the success of restored plant communities.
2. We examined how bird communities responded to the presence and removal of the invasive understorey tree *Pittosporum undulatum* Vent. (sweet pittosporum) in matched woodland areas in temperate south-eastern Australia that were free of *P. undulatum* invasion, were invaded, or had been cleared up to 14 years prior to our sampling.
3. Overall bird species richness and individual abundance were insensitive indicators, as neither were significantly affected by the presence or removal of *P. undulatum*. However, richness and abundance were sharply lower in and beneath the *P. undulatum* canopies compared to the forest overstorey, pointing to a large structural modification by the invader. Bird community composition changed in fairly consistent ways at multiple sites upon invasion by *P. undulatum*, changes that were partly but not completely reversed by removal of *P. undulatum*. The suite of functional traits of the birds present at the sites was disrupted in idiosyncratic ways at sites invaded by *P. undulatum* and only very weakly restored upon clearing of *P. undulatum*. Functional and diversity indices are dependent on the type of management implemented.
4. We propose that a more nuanced approach to management such that some of the invaded forest in neighbouring areas is retained while new trees become established in the cleared areas, providing access to suitable habitat for birds during the transition phase. Such measures are challenging in terms of management and funding but are necessary to maintain avian diversity during and after restoration processes.

KEYWORDS

bioindicators, community functional traits, ecological restoration, *Pittosporum undulatum*

1 | INTRODUCTION

Restoration ecology is increasingly applied to counter the effects of invasive plant species and rescue the original functioning of the ecosys-

tems. Successful restoration is, however, more complex than merely the removal of invasive plant species; the consequence of vegetative restoration for wildlife must also be considered (Munro et al., 2011). Birds are highly integrated wildlife components in any ecosystem

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because they are strongly affected by vegetation structure and floristic richness (Carignan & Villard, 2002; Padoa-Schioppa et al., 2006; Ortega-Álvarez & Lindig-Cisneros, 2012; Munro et al., 2011) and, in turn, contribute to seed dispersal, increased seed germination via gut passage, pollination, pest species control and soil formation, for example through soil turn over and nutrient-rich faecal deposits (Lindenmayer et al., 2017; Reid et al., 2014; Sekercioglu, 2006). Birds, therefore, make excellent bio-indicators of environmental health, particularly because they react rapidly to alterations in environmental conditions (Morrison et al., 2010; Rey-Benayas et al., 2010). Birds have increasingly been incorporated into restoration monitoring around the world (Aerts et al., 2008; Ortega-Álvarez & Lindig-Cisneros, 2012; Reid et al., 2012, 2014; Zahawi & Augspurger, 2006).

Here we investigate the effects of the invasive weed tree, *Pitosporum undulatum* (sweet pittosporum), and its removal on the richness, abundance and functional traits of resident bird communities. There has been some consideration of the interaction of *P. undulatum* with particular bird species (Gleadow, 1982; McNabb & McNabb, 2011), but not with bird communities more broadly. *P. undulatum* is a shade-tolerant tree native to coastal forests of south-eastern Australia that has become invasive throughout temperate Australia, including some regions of its natural territory where it is considered to perform the function of an invader (Gleadow & Ashton, 1981; Gleadow et al., 1983). The presence of a dense *P. undulatum* canopy in forest understorey severely alters the structure and floristic composition of invaded habitats, leading to understorey areas with a high proportion of bare ground and a loss of plant species diversity (O'Leary et al.,

2018). As a result, we expect invaded areas less suitable for a number of bird species due to low habitat heterogeneity (Stirnemann et al., 2014).

The ecological role of bird species can be characterized by their functional traits. Such traits reflect environmental tolerances and capacities for resource capture, reproduction, dispersal (McGill et al., 2006; Reich et al., 2003; Westoby et al., 2002) (Table 1). Species trait values can therefore be used to characterize the functional diversity of a community. Despite the traditional focus on species richness to assess ecological communities, greater attention should be given to functional diversity (Lindenmayer et al., 2015). Our hypotheses are (1) that given the density and uniformity of the *P. undulatum* canopy, invaded areas will have a reduction in the range of functional types of birds and (2) given that the removal of *P. undulatum* allows substantial recovery of native plant communities (O'Leary et al., 2018), bird communities would be restored to the types of communities seen in neighbouring remnant vegetation including richness, density and functional diversity.

Changes in bird functional diversity following restoration might provide a different perspective on recovery of community processes, one that emphasizes community resilience, long-term stability and ecosystem functioning (Fischer et al., 2007; Karp et al., 2011; Lindenmayer et al., 2015), which in turn will lead to the need for more nuanced restoration programmes. We propose that restoration programmes may need to be staggered in space and time to allow bird communities to move into new areas before the habitat provided by the coalesced *P. undulatum* canopies is completely removed.

TABLE 1 Study site details including location, vegetation type (ecological vegetation complex, EVC), *P. undulatum* canopy cover prior to removal, (initial cover %), year of removal and elevation. Reference numbers are used in the labels in Figures 2–4

	Site	Location (°S / °E)	Ecological vegetation complex (EVC)	Initial <i>P. undulatum</i> canopy cover (%)	Year of <i>P. undulatum</i> removal	Mean annual rainfall (mm)	Elevation (m)
1	Wonga Park (WP)	37.76 / 145.28	Grassy dry forest	50	2016	807.5	141
2	Greens Bush (GB)	38.42 / 144.96	Damp sands herb-rich woodlands	50	2015	779.4	176
3	Panton Hill (PH)	37.64 / 145.24	Grassy dry forest	70	2014	688.5	181
4	Woods Reserve (WR)	38.29 / 145.09	Lowland forest	50	2012	904.3	91
5	Birdsland Reserve (BR)	37.92 / 145.34	Grassy dry forest	30	2011	1113.6	170
6	Glenfern Valley Bushlands (GFVB)	47.91 / 145.31	Valley grassy forest	60	2010	1056.8	187
7	Ferntree Gully (FTG)	37.88 / 145.31	Grassy dry forest	50	2006	928.4	276
8	Red Hill (RH)	38.40 / 145.04	Herb-rich foothill forest	60	2006	1008.9	114
9	Montrose (M)	37.82 / 145.35	Grassy dry forest	60	2005	1031.9	409
10	Sherbrooke Forest (SF)	37.90 / 145.37	Wet forest	50	2002	1261.5	495

2 | MATERIALS AND METHODS

2.1 | *Pittosporum undulatum*

Pittosporum undulatum Vent. (Pittosporaceae) occurs naturally across a range of habitat types in eastern and southern Australia, most commonly in wet and temperate rainforests (Gleadow & Ashton, 1981). Altered fire regimes, introduced vectors, peri-urban disturbance and horticultural propagation have contributed to the spread of this species after European arrival in the 1800s (Gleadow, 1982; Gleadow & Ashton, 1981; Gleadow & Narayan, 2007; Gleadow & Rowan, 1982; Gleadow et al., 1983). Presently, *P. undulatum* is invasive within many regions across Australia, from the subtropics to the cool temperature regions of Australia and including isolated regions such as Lord Howe Island and Norfolk Island (Yarra Eurobodalla Council, 2017; Ranges, 2017; Mornington Peninsula Shire, 2012). *P. undulatum* is also becoming problematic globally, with invasive populations in New Zealand, Portugal, Jamaica, Hawaii and South Africa (Gleadow & Ashton, 1981; Goodland & Healey, 1996; Hortal et al., 2010; Lourenço et al., 2011; Mokotjomela et al., 2013). *P. undulatum* establishes quickly after disturbance (Bellingham et al., 2005; Rose & Fairweather, 1997), although infestations can occur at undisturbed locations (Gleadow & Ashton, 1981; Gleadow & Walker, 2014; Rose, 1997). Gleadow (1982) reports that *P. undulatum* fruits are not widely eaten by birds native to the immediate area; however, they represent a major winter food source for the introduced European blackbird (*Turdus merula*), which is thought to be a vector of dispersal, at least in southern Australia (Gleadow, 1982). Once established, mature trees can reach heights of 8–30 m (Mullett, 2001). Individuals form dense crowns, shading out the undergrowth and reducing structural diversity, floristic composition and the integrity of ecological systems (Gleadow & Ashton, 1981; Mullett, 2001).

2.2 | Site selection

Ten sites across peri-urban areas of Melbourne, in south-eastern Australia, were selected to evaluate their bird communities (Table 1). The vegetation at these sites has been surveyed and analysed in a previous study (O'Leary et al., 2018). Sites were selected to contain (1) an area of uninvaded, remnant vegetation supporting a *Eucalyptus* overstorey of varying species composition consistent with local conditions ('reference control'); (2) an area currently infested by *P. undulatum* ('invaded'); and (3) a formerly invaded area where *P. undulatum* had been removed ('cleared'). Two sites (Ferntree Gully and Sherbrooke Forest) lacked invaded patches but are included here for analyses that do not depend on a sequence from control to invaded to cleared patches. Patches of the three vegetation types enable an assessment of both the direction and magnitude of change in bird communities due to invasion and management (Guido & Pillar, 2017).

As we are assuming a space-for-time substitution, we used Ecological Vegetation Class (EVC) mapping supported by on-ground obser-

vations to ensure that the vegetation patches within each site supported similar vegetation (DELWP, 2017). Sites ranged in size from 1 to 12 ha. The management area at each site was characterized as having a severe *P. undulatum* infestation (30–70% canopy cover) prior to removal work (Table 1). With the exception of the Wonga Park site, which was cleared in 2016, all sites had experienced some degree of follow-up weed control within 12 months of the initial *P. undulatum* removal, and all sites cleared for three years or more had received maintenance at least twice. The reference controls at approximately half of the sites had been exposed to control burns within the past 15 years as a means of maintaining the natural disturbance regime and stimulating biodiversity (Penman et al., 2011). Unlike some other studies (e.g. Gleadow & Narayan, 2007), fire was not used in the initial control of *P. undulatum* at our sites. Cleared and invaded areas had not been burnt within the timeframe of this study (14 years). Further details of the vegetation at each site can be found in O'Leary et al. (2018). Information on the density of *P. undulatum* at the cleared areas, weed management practices and disturbance regime was included in the analysis.

2.3 | Bird surveys

Bird surveys were conducted on three separate mornings at each site from mid-May to late June of 2017. Surveys were conducted within the first 3 h after sunrise, following a modified version of the process established by Loyn (1986) and outlined in Loyn et al. (2007), that is 10 min of surveying time was implemented for each hectare of sampling area at each site, to a maximum of 20 min. This timeframe has been observed as appropriate to survey bird communities within south-eastern Australian forests, whilst reducing the risk of bias towards conspicuous species with distinctive and/or frequent calls. One of us (BO'L) was present for each survey at each site, supported by volunteer surveyors experienced with local bird communities. All birds observed by sight and call within and below the vegetation canopy were identified to species level. Birds flying overhead were not included in the study. Bird species relative abundance was determined by dividing the total number of birds observed over the three surveys at each site. Surveys distinguished bird use of the habitat within or below the *P. undulatum* canopy (PU) from use of the overstorey (NPU, not PU) due to the predicted large effects of dense *P. undulatum* canopies. Density was determined by dividing the numbers of birds by the area surveyed.

2.4 | Functional traits

Values of five traits reflecting ecological functionality (life history, habitat preference and feeding guild) were extracted for each bird species identified in our surveys from the *Handbook of Australian, New Zealand and Antarctic Birds* (Higgins et al., 2006). The traits and brief descriptions of their ecological relevance are listed in Table 2.

TABLE 2 Functional traits collected for each bird species observed within the study

Trait	Trait Description	Reference
Body mass (g)	Smaller birds are associated with heterogeneous, fine-grained vegetation structure, while larger birds are more commonly found in open environments	Fischer et al. (2008), Stirnemann et al. (2014)
Foraging behaviour (arboreal or non-arboreal)	Ground foraging species are associated with heterogeneous and high ground cover, potentially as protection against predation	Antos et al. (2008), Stirnemann et al. (2014)
Nest location (arboreal or non-arboreal)	Arboreal nests are more subject to predation within south-eastern Australian eucalypt forests, particularly by other bird species	Piper and Catterall (2004), Whyte et al. (2005)
Feeding guild	Insectivores, omnivores, carnivores, nectivores/granivores/frugivores	Green (1997)
Interspecific interactions (aggressive or nonaggressive)	Many honeyeaters (Meliphagidae) and some carnivorous species are strongly territorial and can suppress overall bird diversity	Ford (1979), Ford et al. (2001), Fulton and Ford (2002)

2.5 | Statistical analysis

Differences in bird species richness and individual abundance among reference invaded and cleared vegetation types and between the *P. undulatum* understorey and overstorey in invaded sites were tested with one-way ANOVAs. To compare species richness in individual feeding guilds across the three vegetation types, we used Kruskal–Wallace tests, due to the smaller numbers of species involved in each guild. The effect of time since *P. undulatum* removal was tested with linear regression on relativized measures of species richness and individual abundance (richness or abundance in cleared patch divided by richness or abundance in the corresponding reference control). To summarize the differences and similarities among bird communities in the three vegetation types, we employed principal components analysis (PCA) of bird species presence/absence data using the `prcomp` function in R (R Core Team, 2017). Loadings on the first two principal components were examined to account for the contribution of individual species to the community configuration. We repeated the PCA using bird abundance data using nonmetric multi-dimensional scaling and checked that the results were biologically meaningful as suggested by Björklund (2019). Since all results were in qualitative agreement, we present PCA of the presence–absence data here. Scores on the first two principal components were compared among reference, invaded, and cleared vegetation types using Wilcoxon signed-rank tests.

The PCA was also used to investigate the functional response of bird communities to *P. undulatum* infestation and removal. Mean functional trait values in the species assemblage were calculated from the traits of individual species weighted by the abundance of individuals of the species. All data were centred and scaled to unit variance prior to analysis. All analyses were conducted using the R statistical platform (R Core Team, 2017).

3 | RESULTS

Overall species richness and abundance of birds varied widely among sites and vegetation conditions, but no significant differences occurred among reference, invaded, and cleared vegetation (ANOVA test of the

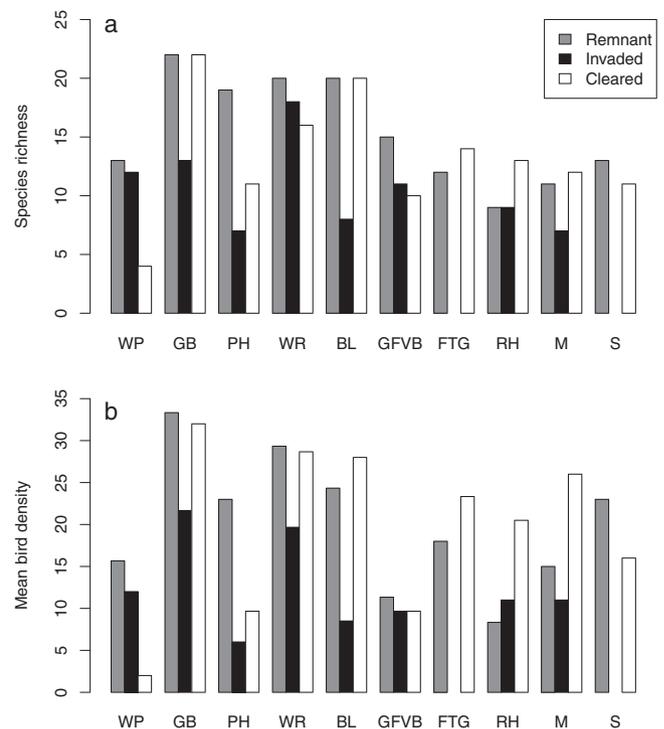


FIGURE 1 Species richness (a) and densities of birds (b) observed within vegetation types. Grey bars: reference control (remnant vegetation); Black bars: invaded by *P. undulatum*; open bars: cleared area, *P. undulatum* removed. Data for individual sites can be found in Supporting Data File 1

effect of vegetation type on species richness (Figure 1a): $F_{2,25} = 2.44$, $p = 0.11$; on bird abundance (Figure 1b): $F_{2,25} = 2.40$, $p = 0.11$).

In total, 47 different bird species were observed across all study sites. The remnant section of the Greens Bush site provided the greatest diversity with 22 separate species, whilst only four species were observed in the area invaded by *P. undulatum* at Woods Point. The brown thornbill (*Acanthiza pusilla*) was the most abundant species across all sites, whilst a number of birds were observed only once throughout the study. Few exotic species contributed to these numbers: only three non-native species were observed across all sites. The

only threatened species recorded was the powerful owl, *Ninox strenua* (Webster et al., 1999): two individuals were observed in reference controls of the Woods Reserve site and a further two birds observed within the cleared area of the Birdsland Reserve site.

Within patches invaded by *P. undulatum*, both richness and abundance differed significantly between the bird communities in and under the *P. undulatum* canopy and those in the *Eucalyptus* overstorey above (species richness: $F_{1,14} = 7.1$, $p = 0.018$; abundance: $F_{1,145} = 10.6$, $p = 0.005$). There were an average of 49% fewer species and 64% fewer birds in and under *P. undulatum* canopies compared to the overstorey. At invaded sites, the *Eucalyptus* overstorey remains until either the trees die, or in some cases is overtopped by the *P. undulatum*, but does not reform. No *Eucalyptus* seedlings have ever been observed growing under a canopy of *P. undulatum* (Gleadow & Ashton, 1981; Gleadow & Walker, 2014; Naryan et al.; O'Leary et al., 2018).

Following the removal of *P. undulatum*, species richness and abundance appeared to rebound slowly, reflecting the time since clearing (Figure 2). Although there was no overall statistically significant time effect (linear regression model for relative species richness, $F_{1,8} = 4.4$, $p = 0.069$; for relative abundance, $F_{1,8} = 3.6$, $p = 0.095$), this result was due to a single site, Sherbrooke Forest. It is the highest and wettest of the study sites (Table 2) and the first to be cleared, giving it high leverage in the regression analysis. Without the Sherbrooke Forest site, regressions for the remaining nine sites would be statistically significant (relative species richness, $F_{1,8} = 9.6$, $p = 0.017$; relative abundance, $F_{1,8} = 15.6$, $p = 0.0056$). Time, therefore, may affect the species richness and abundance of birds in post-clearance vegetation in most instances, but the effect would seem not to be universal.

There was a largely coherent, repeated response of bird communities to *P. undulatum* invasion, as shown by PCA of species presence/absence (Figure 3a). In most cases, *P. undulatum* invasion tended to shift the bird community in one direction along the first principal component (negative shifts in Figure 3, although sign is arbitrary in principal component scores), while clearing tended to shift the community back. However, this recovery seldom left the post-clearing assemblage similar to the control assemblage, as indicated by separation of pre- and post-invasion communities on the second principal component. Sites 1 and 4 were exceptions to the general pattern, but the negative-then-positive pattern of shifts along PC1 was statistically detectable. Shifts between reference and invaded patches differed significantly from the corresponding reverse shifts between invaded and cleared patches (Wilcoxon signed-rank test, $p = 0.023$). Shifts along PC2 were less coordinated, and the reference-to-invaded shifts were not significantly different from the invaded-to-cleared shifts (Wilcoxon signed-rank test, $p = 0.21$).

Some species, particularly the Australian magpie, *Gymnorhina tibicen* (Gt), golden whistler, *Pachycephala pectoralis* (Pp1), spotted pardalote, *Pardalotus punctatus* (Pp2), and grey butcherbird, *Cracticus torquatus* (Ct), influenced the PCA because their presence distinguished sites 2, 4, and 5 from the others, although they were little affected by *P. undulatum* at these sites (Figure 3b; see Table 2 for site information). The varied sitella, *Daphoenositta chrysoptera* (Dc), and mistle-

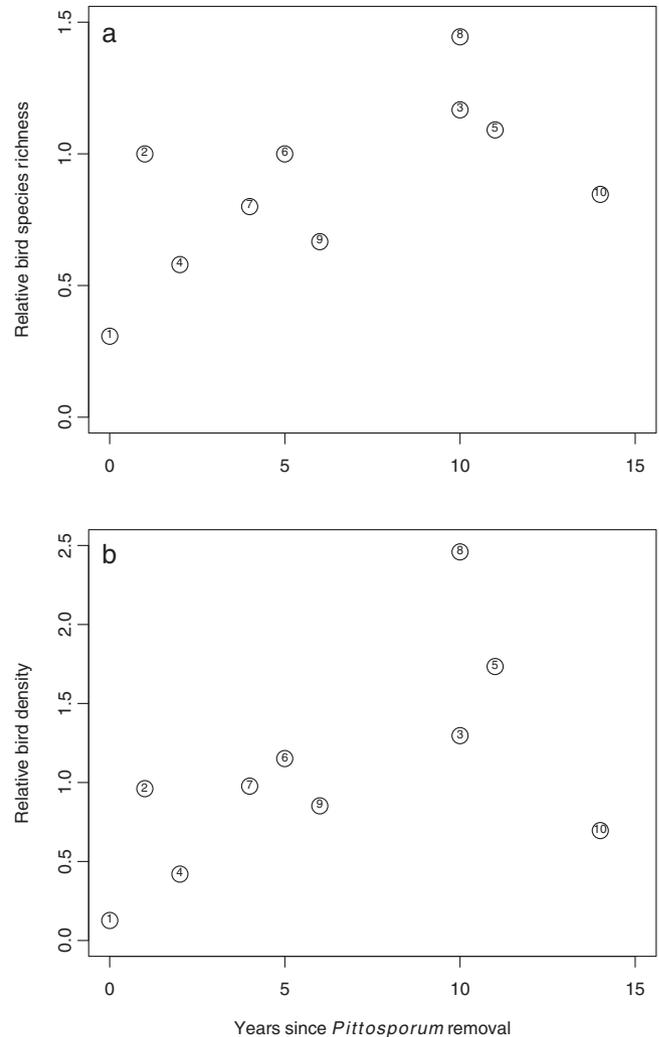


FIGURE 2 Effect of time since *P. undulatum* removal on (a) relative species richness and (b) relative abundance (richness or abundance in cleared patch divided by richness or abundance in the corresponding reference control). Numbers within symbols refer to site numbers in Table 2

toe bird, *Dicaeum hirundinaceum* (Dh), were unique to site 4 and also had strong influence (Figure 3b). The shifts from remnant controls to invaded plots to cleared plots were strongly influenced by two types of birds: ground-feeding and/or nesting specialists, such as the white-browed scrubwren, *Sericornis frontalis* (Sf), superb fairywren, *Malurus cyaneus* (Mc), little raven, *Corvus mellori* (Cm), and magpie lark, *Grallina cyanoleuca* (Gc); and carnivorous hunters such as the laughing kookaburra, *Dacelo novaeguineae* (Dn), and powerful owl, *Ninox strenua* (Ns) (Figure 3b). Both the ground specialists and carnivores tended to disappear from vegetation invaded by *P. undulatum*.

The effect of *P. undulatum* is especially pronounced when bird communities are viewed as assemblages of feeding guilds, habitat preferences and life-history traits. All reference control patches host a relatively similar array of functional traits, as shown by PCA (Figure 4a). *P. undulatum* invasion disperses the functional assemblages outward in

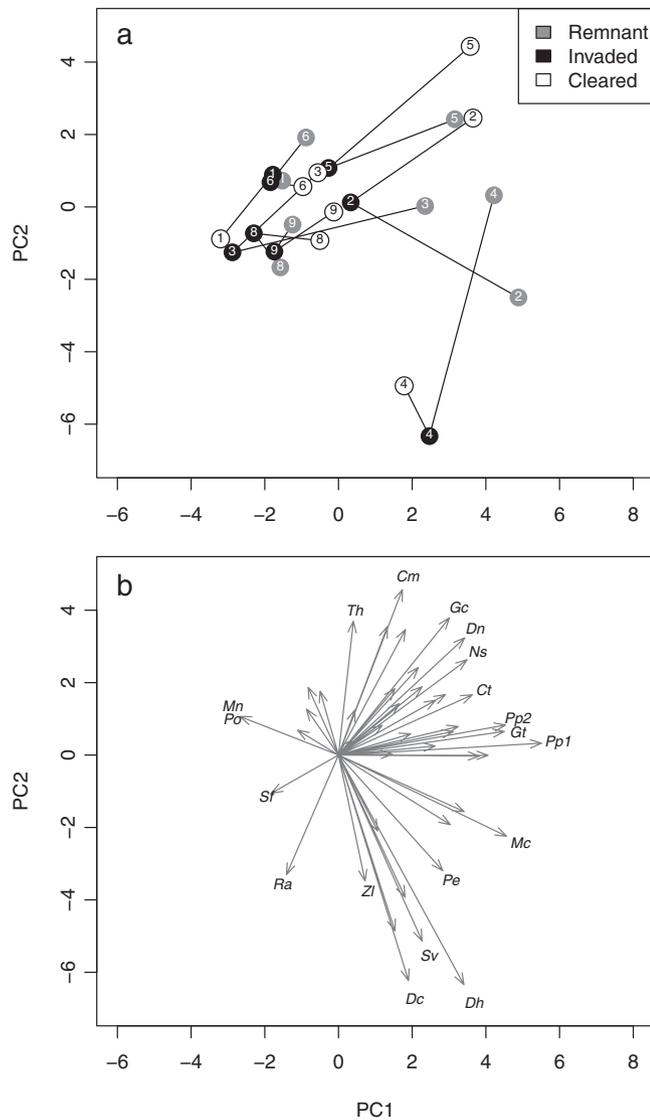


FIGURE 3 Principal components analysis of the effect of *P. undulatum* invasion and subsequent removal on bird communities. (a) Plane of first two principal components based on bird species presence/absence. Data for bird species at individual sites can be found in Supporting Data File 2. PC1 accounted for 12.1% and PC2 9.8% of the total variation. Grey symbols = reference control vegetation; black symbols = invaded vegetation; open symbols = cleared vegetation. Numbers correspond to sites listed in Table 2. (b) Loadings of individual species on the first two principal components. Species with large influence are labelled as follows: Cm, *Corvus mellori* (Little Raven); Ct, *Cracticus torquatus* (Grey Butcherbird); Dn, *Dacelo novaeguineae* (Laughing Kookaburra); Dc, *Daphoenositta chrysoptera* (Varied Sitella); Dh, *Dicaeum hirundinaceum* (Mistletoebird); Gc, *Gallina cyanoleuca* (Magpie Lark); Gt, *Gymnorhina tibicen* (Australian Magpie); Mc, *Malurus cyaneus* (Superb Fairywren); Mn, *Menura novaehollandiae* (Superb Lyrebird); Ns, *Ninox strenua* (Powerful Owl); Pp1, *Pachycephala pectoralis* (Golden Whistler); Pp2, *Pardalotus punctatus* (Spotted Pardalote); Pe, *Platycercus eximius* (Eastern Rosella); Po, *Psophodes olivaceus* (Whipbird); Ra, *Rhipidura albiscapa* (Grey Fantail); Sf, *Sericornis frontalis* (White-browed Scrub Wren); Sv, *Strepera versicolor* (Grey Currawong); Th, *Trichoglossus haematodus* (Rainbow Lorikeet); Zl, *Zosterops lateralis* (Silvereye). Loadings for all species are given in Supporting Data File 3 (P-A.loadings.Fig3b.csv)

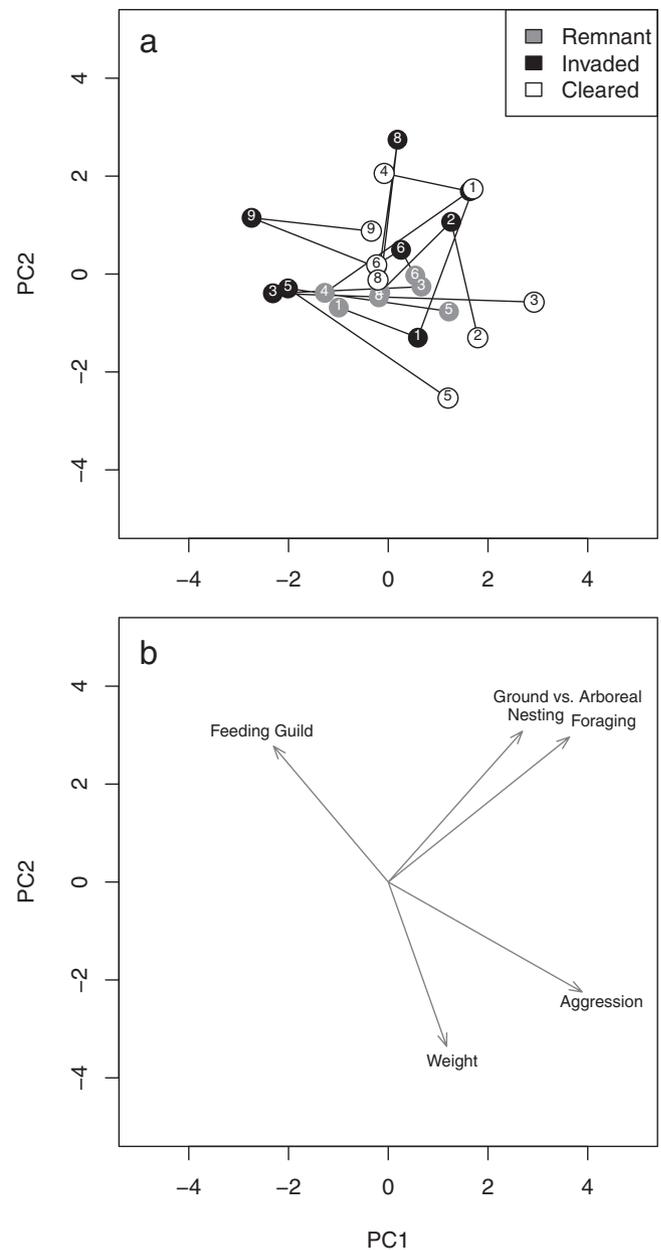


FIGURE 4 Principal components analysis based on functional traits of bird species (see Table 2 for list of traits). (a) Plane of first two principal components. PC1 accounted for 34.7% and PC2 26.2% of total variation. (b) Loadings of individual traits on the first two principal components. Loadings are given in Supporting Data File 4. (FunctionalTrait.loadings.Fig4b.csv). Symbols and site numbers as in Figure 3

the plane of the first two principal components, while removal brings further pronounced change, but only at site 8 does the post-removal assemblage of functional traits resemble that of the control (Figure 4). The PCA loadings suggest that all traits contribute roughly equally to the pattern, although a ground-arboreal distinction in both nesting and foraging had correlated effects (Figure 4b). Feeding guilds were a distinctive contributor to these changes. Invasion by *P. undulatum* tended not to greatly affect the species richness in three of the

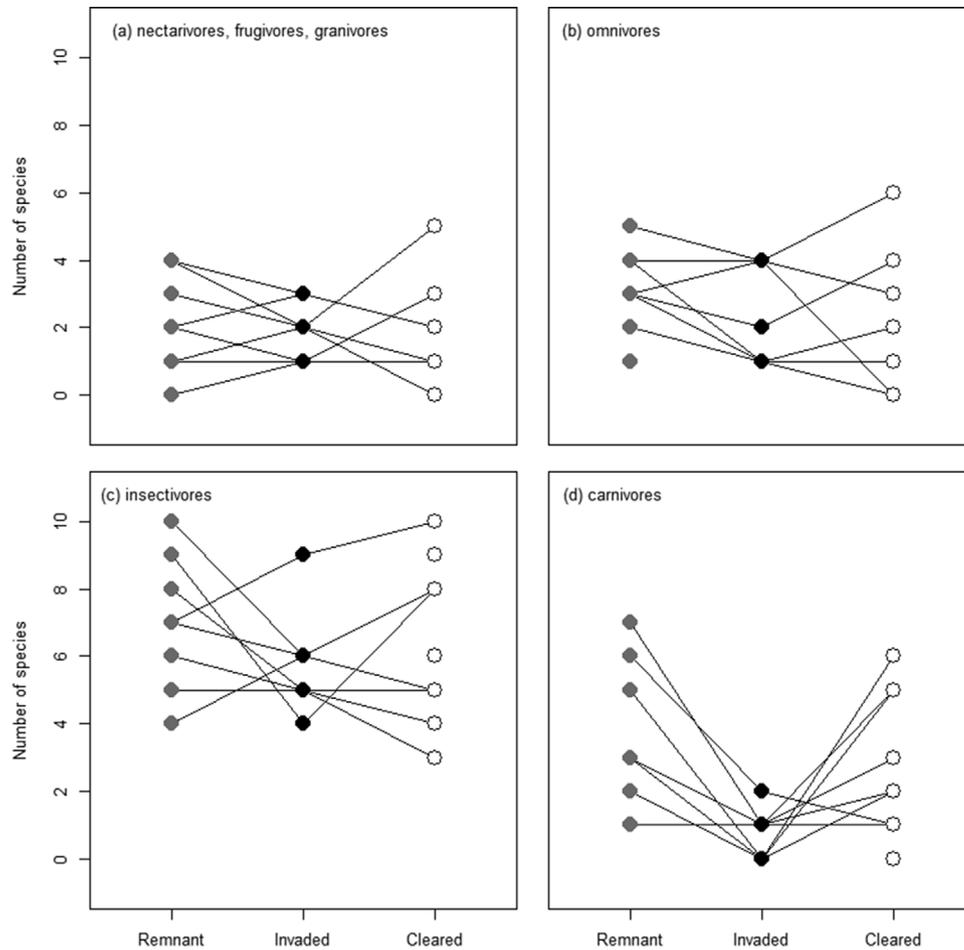


FIGURE 5 Effect of *P. undulatum* on abundance of species in four feeding guilds present at the ten sites listed in Table 1. (a) Nectarivores, frugivores and granivores; (b) omnivores; (c) insectivores; (d) carnivores. Grey symbols = reference control (remnant) vegetation; black symbols = invaded vegetation; open symbols = cleared vegetation. Lines connect vegetation types at the same site; unconnected symbols represent sites 7 and 10 from Table 1, which had no *Pittosporum*-invaded vegetation

four guilds we delineated, but sharply reduced the number of carnivorous species present at most sites (Figure 5). Species numbers did not differ significantly among control, invaded and cleared habitats in the nectarivore-frugivore-granivore guild (Kruskal-Wallis $\chi^2 = 1.04$, $d.f. = 2$, $p = 0.59$), the omnivore guild ($\chi^2 = 2.16$, $d.f. = 2$, $p = 0.34$) or the insectivore guild ($\chi^2 = 2.12$, $d.f. = 2$, $p = 0.34$). However, the loss of carnivorous bird species in *P. undulatum*-invaded patches and rebound in cleared patches (Figure 5d) produced a significant difference in richness ($\chi^2 = 11.01$, $d.f. = 2$, $p = 0.004$), an effect detectable also in the loadings of the powerful owl (Ns) and laughing kookaburra (Dn) on the second principal component in Figure 3b, which tended to separate the bird communities in control and cleared vegetation.

4 | DISCUSSION

P. undulatum profoundly alters the structure of vegetation in the landscapes it invades (Gleadow & Ashton, 1981; O'Leary et al., 2018; Rose & Fairweather, 1997). We found here that bird communities are also

different in areas invaded by *P. undulatum*, although the effects are not readily apparent at the level of species richness or bird abundance (Figure 1) and could be overlooked with less systematic observations. Cleared, remnant and invaded areas differed in species composition and the functional traits of the present bird assemblages (Figures 3 and 5), the most obvious being the decrease in carnivorous species in the invaded sites. Some bird species were present only in the remnant or cleared plots, while others, such as the white-throated treecreepers, grey fantails and white-browed scrubwren, were relatively resilient to *P. undulatum* invasion. The latter group are all relatively small, insectivorous species, and there may be trade-offs between the protection afforded by the dense canopy and the increased floristic diversity in the treated site. In contrast, species such as the rainbow lorikeet (Th, a nectarivore), little raven (Cm, an omnivore), varied sittella (Dc, a branch-gleaning insectivore) and mistletoebird (Dh, a frugivore) were more sensitive to the long-term effects of *P. undulatum* invasion even after clearance and contributed strongly to the differences between communities in control and cleared habitats (as indicated by strong loadings on PC2 in Figure 3b).

4.1 | Overall bird richness and abundance did not differ among vegetation types

It is striking that neither bird species richness nor abundance differed significantly among reference, invaded and cleared areas, given that a relationship between habitat structure and avian richness is well established (Ikin et al., 2012; MacArthur & MacArthur, 1961; Recher, 1969; Stirnemann et al., 2014). Foliage, flowers, bark, ground plants, air spaces and tree hollows have been identified as important habitat features for birds (Antos et al., 2008; Ikin et al., 2012; McElhinny et al., 2006; Stirnemann et al., 2014). In particular, ground vegetation, woody debris and logs support an invertebrate fauna that acts as a foraging substrate for many bird species (Antos & Bennett, 2005; McElhinny et al., 2006). Invasion greatly reduces plant growth beneath the dense *P. undulatum* canopy (Gleadow & Ashton, 1981; Mullett & Simmons, 1995; O'Leary et al., 2018; Recher et al., 2002; Stirnemann et al., 2014), and both species richness and abundance of birds were sharply reduced in and under *P. undulatum* canopies relative to the overstorey at invaded sites. But other than the near absence of a shrub/ground layer in invaded patches and a regenerating layer after clearance, many of the habitat components required by native birds are likely to remain, particularly in the intact *Eucalyptus* overstorey. Invaded sites seem, therefore, to be able to support abundant bird communities.

Two important considerations constrain this optimistic conclusion, however. The first is that ground foraging birds, which form some of the most abundant bird communities in temperate Australia (Antos et al., 2008; McElhinny et al., 2006), may have suffered long-term decline apart from any effect of *P. undulatum* (Antos et al., 2008; Ford, 2011; Ford et al., 2001; Stirnemann et al., 2014). Fragmentation of landscapes along with urbanization and the introduction of invasive mammalian predators, especially foxes and cats, has resulted in the gradual reduction of ground-dwelling bird species from many temperate *Eucalyptus* forest and woodlands (Antos & Bennett, 2005; Antos et al., 2008; Ford, 2011). Recovery of ground vegetation following removal of *P. undulatum* may not attract a large avian fauna if ground-dwelling bird species richness is compromised at a regional scale.

The second consideration is that even if a *Eucalyptus* overstorey provides suitable habitat for many native species despite a high *P. undulatum* density, invasive populations of this species dramatically limit the germination of *Eucalyptus* seedlings, resulting in the virtual absence of younger *Eucalyptus* age classes able to replace the mature stock (Gleadow & Walker, 2014). The *Eucalyptus* overstorey persists in the invaded area until the trees die and does not reform. *Eucalyptus* seedlings have never been observed to grow under a canopy of *P. undulatum* (Gleadow & Ashton, 1981; Gleadow & Narayan, 2007; Gleadow & Walker, 2014; O'Leary et al., 2018). Therefore, the quality of habitat structure is likely to become increasingly diminished at invaded sites as the overstorey trees age and eventually die.

4.2 | Speed of recovery of the shrub- and ground-level habitat limits the recovery of bird communities

Most bird communities experienced similar changes when *P. undulatum* invaded a site and when it was removed. The trajectories between reference control patches and invaded patches along the first principal component of a PCA were similar among most sites, as were reversals when patches become cleared (Figure 3). However, the restoration of bird community composition following the removal of *P. undulatum* was usually incomplete. Sites 5, 6 and 9 (Montrose, Birdland Reserve and Glenfern Valley Bushlands) had the most similar communities in reference and cleared patches, but differences between reference and cleared patches at other sites were considerable. These differences may persist because the speed of recovery of the shrub- and ground-level habitat limits the recovery of bird communities, especially ground-dwelling birds. We found some indication of such a rate-limited recovery in bird communities in the effect of time since clearance on species richness and individual abundance (Figure 2), although the marginal statistical significance points to the clear need for more evidence before firm conclusions can be drawn.

In this study, the presence of *P. undulatum* appeared to have a greater disruptive effect on the functional traits present in bird communities rather than on species composition. Reference areas supported similar functional composition, while invaded sites were displaced in all directions on the plane of the first two principal components. Cleared areas did not typically return to locations near their corresponding reference patches (Figure 4). Further work expanding the functional traits used in the analysis would help establish how repeatable the effects of *P. undulatum* are, but we emphasize the ecological relevance of the traits we examined (Table 2).

One notable change in the functional traits present in a community is the reduction in the number of carnivorous bird species when *P. undulatum* is present (Figure 5). A carnivore's view of prey is likely to be restricted by the dense foliage of a *P. undulatum* canopy (Stirnemann et al., 2014), impeding the foraging of larger species such as carnivorous magpies (*Gymnorhina tibicen*) and pied currawongs (*Strepera graculina*), as well as large territorial honeyeaters such as bell miners (*Manorina melanophrys*) and noisy miners (*M. melanocephala*) (Ford, 1979, 2011). Smaller birds are more commonly associated with complex, heterogeneous and fine-grained vegetation (Holling, 1992; Fischer et al., 2008; Stirnemann et al., 2014). Thus, the discontinuity in vegetation texture created by *P. undulatum* appears to strongly limit the kinds of behavioural and life-history traits that can be supported.

Four powerful owls were sighted in two separate locations in our survey. Owls were sighted roosting in a mature messmate, *Eucalyptus obliqua*, in the reference control at Woods Reserve, and in mature blackwoods, *Acacia melanoxylon*, in the area cleared of *P. undulatum* six years earlier at Birdland Reserve. Both tree species are indigenous to the area. Reports have suggested that *P. undulatum* may provide important habitat for the powerful owl (*Ninox strenua*), a threatened

native species in Victoria (McNabb & McNabb, 2011). The key factor appears to be the provision of canopy cover for roosting rather than foraging (McNabb & McNabb, 2011). While forest trees can also supply this need, there is a danger that lack of cover after clearing the invasive *P. undulatum* could be detrimental to these birds, creating some hesitancy around restoration programmes (McNabb & McNabb, 2011). It is noteworthy that, in the present study, we did not observe any powerful owls in areas invaded by *P. undulatum*. Our results, albeit based on limited observations, suggest that powerful owls find suitable habitat in areas where invasive tree control has been implemented. The retention of established tall canopy and subcanopy trees suitable for roosting in neighbouring areas is thus likely to be important to ensure continuity of habitat for this species.

Only three out of the 47 bird species observed (6.38%) throughout the study were exotic species and all at relatively low abundance. Despite reports suggesting European blackbirds may be a common seed dispersal vector of *P. undulatum* (Gleadow & Rowan, 1982), no difference in presence or abundance of this or other exotic species was found across the three vegetation types. This supports the hypothesis that it is the juxtaposition of habitats preferred by blackbirds, such as lawns and open areas, that promotes dispersal by these introduced avian vectors, rather than the presence of *P. undulatum* alone (Gleadow & Ashton, 1981; Gleadow, 1982). The role of exotic and native birds in seed dispersal and continuing invasion and re-invasion by *P. undulatum* warrants further study (Gleadow, 1982).

4.3 | Birds as indicators in restoration management and implications for practitioners

Birds offer insights into restoration management distinct from those uncovered by monitoring vegetation alone (Munro et al., 2011). The rate and scale of restoration programmes can affect the types of bird communities that are able to either remain or recolonize particular areas, affecting density, diversity, and functional groups. Restored sites often vary in vegetation composition and structure independently of their time under management (Batisteli et al., 2018). While the outcomes from this study have potential to improve other restoration management programmes focused on invasive trees, the effect of invasive tree removal will likely differ depending upon the habit and ecology of the trees in question, together with their relationship with the surrounding environment. Attention to bird communities and focal species can improve our capacity to monitor the effects of invasive tree removal and other restoration efforts.

Information gathered here offers details distinct from those uncovered from a monitoring programme focusing specifically on vegetation alone, and that the richness, abundance and functionality of birds in invaded sites should be taken into consideration when designing and evaluating the efficacy of ecological restoration programmes. In our case, it is essential that habitat is maintained for the threatened powerful owl. In order to do this, management must be slow and sensitive and carried out in patches over a 5–10 year period, or even longer. This

retains some of the invaded forest in adjacent areas to provide habitat in the transitional phase while new trees become established and become tall enough. Leaving dead trees left from 'drill and fill' strategies also provides habitat while the vegetation recovers. Such approaches are extremely difficult given the nature of funding for management that tend to drive short-term interventions on a wide scale. It is also challenging from the perspective of amenity and safety: leaving many dead trees could be perceived as ugly, they may become a fire hazard and may even be in danger of falling on people in areas that are accessed by humans.

While the outcomes from this study have potential to improve the management of other restoration programmes focused on invasive trees, the effect of invasive tree removal will differ depending upon the habit and ecology of the trees in question, together with their relationship with the surrounding environment. We recommend that a monitoring programme similar to that presented here is conducted to improve the capacity of invasive tree removal projects, to help in the design of the programme to ensure there is transitional habitat to help maintain biodiversity values and to assess the effects of restoration efforts.

5 | CONCLUSION

In this study, we compared the functional diversity, density and species richness of bird communities in areas invaded by *P. undulatum* with areas that had been managed to remove this woody weed, and adjacent remnant areas. We found that while clearing tended to shift the community back towards that found in the remnant sites, this recovery seldom left the post-clearing assemblage similar to the control assemblage. We conclude that the richness, abundance and functionality of birds in invaded sites should be taken into consideration when designing and evaluating the efficacy of ecological restoration programmes.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

BO'L designed the study and collected the data. RG led the overall project. RG, SV and MB contributed to the design of this particular study. Data were analysed by BO'L and MB. BO'L wrote the first draft of the manuscript. All authors contributed critically to the writing of the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.3n5tb2rhj> (Gleadow et al., 2021)

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