Beyond pattern to process: Current themes and future directions for the conservation of woodland birds through restoration plantings

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Beyond pattern to process: Current themes and future directions for the
conservation of woodland birds through restoration plantings

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Abstract

Habitat loss due to land conversion for agriculture is a leading cause of global biodiversity loss and altered ecosystem processes. Restoration plantings are an increasingly common strategy to address habitat loss in fragmented agricultural landscapes. However, the capacity of restoration plantings to support reproducing populations of native plants and animals is rarely measured or monitored. This review focuses on avifaunal response to revegetation in Australian temperate woodlands – one of the world’s most heavily altered biomes. Woodland birds are a species assemblage of conservation concern, but only limited research to date has gone beyond pattern data and occupancy trends to examine whether they persist and breed in restoration plantings. Moreover, habitat quality and resource availability, including food, nesting sites, and adequate protection from predation, remain largely unquantified. Several studies have found that some bird species, including species of conservation concern, will preferentially occupy restoration plantings relative to remnant woodland patches. However, detailed empirical research to verify long-term population growth, colonisation and extinction dynamics is lacking. If restoration plantings are preferentially occupied but fail to provide sufficient quality habitat for woodland birds to form breeding populations, they may act as
ecological traps, exacerbating population declines. Monitoring breeding success and site fidelity are
under-utilised pathways to understanding which, if any, bird species are being supported by
restoration plantings in the long term. There has been limited research on these topics
internationally, and almost none in Australian temperate woodland systems. Key knowledge gaps
centre on provision of food resources, formation of optimal foraging patterns, nest predation levels
and the prevalence of primary predators, the role of brood parasitism, and the effects of patch size
and isolation on resource availability and population dynamics in a restoration context. To ensure
that future restoration plantings benefit woodland birds and are cost-effective as conservation
strategies, the knowledge gaps identified by this review should be investigated as priorities in future
research.

Introduction
A large fraction of the world’s woodland and forest avifauna is declining (IUCN 2016; Waldron
et al. 2017), reflecting the well-documented global trend of biodiversity loss associated with
intensifying anthropogenic activities (Butchart et al. 2010). An increasingly common strategy to
address habitat loss in fragmented agricultural landscapes is the creation of habitat through
 revegetation, often referred to as “restoration plantings” (Pastorok et al. 1997; Cairns 2000; Rey
Benayas et al. 2009; Barral et al. 2015). These are typically small patches of planted native
vegetation, and are often intended to facilitate landscape connectivity and conservation of fauna
such as birds (Block et al. 2001; Freudenberger 2001). Patterns of bird species occupancy and
abundance in restoration plantings are commonly used to infer habitat quality (Cunningham et al.
2008; Munro et al. 2011; Lindenmayer et al. 2012). However, there has been limited research on
the population responses of birds to restoration plantings or other forms of habitat restoration, such
as remediation (Larison et al. 2001; Germaine and Germaine 2002). It is crucial to understand the
population dynamics of birds in revegetated landscapes to establish whether restoration plantings
provide quality habitat in which birds can survive and reproduce. This is particularly relevant for
threatened and declining bird assemblages that may come to rely on restoration plantings for long-
term population stability.

The ecological value of temperate woodland restoration plantings for woodland birds in Australia
has traditionally been assessed using pattern data – primarily presence and abundance of bird
species in study sites. This pattern-based research (e.g. Table 2) provides a critical basis for
understanding the potential value of restoration plantings for woodland birds in fragmented
environments. However, to supplement the existing body of knowledge, a much deeper
understanding is needed of the demographic and behavioural responses (survival, site fidelity,
breeding success, dispersal, etc.) of woodland bird populations to habitat restoration. This is fundamental to determine the conservation and management value of restoration plantings, including their potential contribution to reversing species declines (Bennett and Watson 2011). For example, species that have been classified as ‘planting specialists’ (Table 1) may be expected to successfully breed in restoration plantings, but this has not been adequately tested. It is therefore essential to begin to explore these processes in a restoration context, asking, ‘Do restoration plantings facilitate the long-term persistence of birds in fragmented landscapes?’

Previous research on bird community population dynamics, such as breeding success, has mostly dealt with birds in remnant habitat (e.g. Hoover et al. 1995; Zanette and Jenkins 2000; Berry 2001; Zanette 2001; Herkert et al. 2003; Debus 2006a; Debus 2006b; Holoubek and Jensen 2016), with a subset of comparative studies in fragmented and intact landscapes (e.g. Burke and Nol 2000; Cooper et al. 2002; Luck 2003). The majority of earlier work in revegetated landscapes has focused on species richness and abundance, with an emphasis on monitoring for occupancy by birds through time after establishment of restoration plantings (e.g. Taws 2002; Twedt et al. 2002; Martin et al. 2004; Barrett et al. 2008; Saunders and Nicholls 2008; Freeman et al. 2009; Gould 2011; Munro et al. 2011; Becker et al. 2013; Lindenmayer et al. 2016). This earlier research has collectively established that some woodland bird species are able to colonise and occupy restoration plantings. The pressure of potential extinction debts for woodland birds (Ford et al. 2009) – that is, continued declines even after habitat loss and degradation (or other challenges) are eliminated or reversed (Kuussaari et al. 2009) – adds impetus to the need for replacing lost woodland habitat. However, it is imperative the effects of revegetation on avifauna are more comprehensively understood, lest they fail to address (or at worst, exacerbate) population declines.

**Approach**

In this paper, we review the current knowledge on avifaunal response to revegetation and habitat restoration, and provide a general overview and synthesis of existing and future research directions on the topic of woodland birds in restoration plantings. We focus largely on Australian temperate woodlands, the cover of which has been reduced by up to 90% over the past 150 years as a result of land clearing for agriculture (Paton and O’Connor 2010). We build on the preliminary overview by Munro et al. (2007), consolidating the most recent research on the relationship between birds and restoration plantings and examining the available information that underpins practical restoration of woodland habitat. We move beyond the scope of previous reviews by exploring how the implementation of restoration plantings might influence the long-term survival and persistence of woodland bird communities in fragmented agricultural landscapes. Finally, we identify gaps in the
current knowledge and propose further research that would enhance understanding of the population
dynamics of woodland birds in restoration plantings and revegetated landscapes.

We identified relevant literature for this paper by searching publication databases and citation lists,
including ScienceDirect, Scopus and Google Scholar. We took a non-systematic approach and used
a broad range and combination of search terms, including ‘woodland birds’, ‘breeding success’,
‘population dynamics’, ‘occupancy’, ‘distribution’, ‘revegetation’ and ‘restoration’. We searched
the internet and an institutional library catalogue for non-peer-reviewed work including books,
theses and reports.

Background

Habitat degradation and restoration

Temperate woodlands once covered an extensive area of southern Australia, however, the vast
majority has been cleared for agriculture since European settlement (Saunders and Curry 1990;
Lindenmayer et al. 2010a; Bradshaw 2012). Estimates vary, but around 32 million hectares, or up to
90%, of native temperate woodland vegetation cover has been cleared (Vesk and Mac Nally 2006;
Paton and O'Connor 2010). Scattered remnants persist, but due to their isolation and degradation
history, they are vulnerable to threatening processes such as agricultural intensification, grazing,
nutrient enrichment, weed invasion, and climate change (Eldridge 2003; Maron and Fitzsimons

The negative effects of broad-scale habitat clearance on the Australian environment began to be
widely recognised in the 1980s (Saunders et al. 1991; Hobbs and Saunders 2012; Lindenmayer et
al. 2013; Campbell et al. 2017). Changes in attitude towards land management throughout the
1980s and 1990s led to small-scale revegetation programs that were initially instigated by the
farming and environmental sectors to address issues such as salinity and erosion (Stirzaker et al.
2002; Campbell et al. 2017), with larger-scale government-initiated revegetation programs such as
the National Tree Program and the One Billion Trees Program applied within the next two decades
(Hajkowicz 2009; Lindenmayer et al. 2013). Many early plantings were implemented without a
well-defined wildlife conservation plan, but have nonetheless in some cases been occupied by
woodland birds and other fauna (Munro et al. 2007; Lindenmayer et al. 2016).

In more recent years, some restoration plantings have been implemented with clear plans and goals
relating to ecological factors, such as the habitat requirements of focal species (Freudenberger 2001;
Lindenmayer et al. 2013). Knowledge of effective revegetation techniques has also been used to begin construction of large-scale habitat linkage corridors (e.g. Gondwana Link) through the acquisition and revegetation of farming properties (Paton and O'Connor 2010). An ongoing (to 2020), large-scale government initiative is the 20 Million Trees Program, which aims to “improve the extent, connectivity and condition of native vegetation”, with explicit reference to threatened species such as the southern emu-wren (*Stipiturus malachurus*) and regent parrot (*Polytelis anthopeplus*) (Australian Government Department of the Environment and Energy 2017; Landcare Australia 2017). Vegetation is also increasingly being planted for carbon sequestration, and such plantings have the potential to enhance the conservation of biodiversity (Bradshaw et al. 2013; Collard et al. 2013).

With ongoing large-scale revegetation programs such as the 20 Million Trees Program underway in Australia, extensive areas of temperate woodland restoration plantings are being added to the landscape every year (Atyeo and Thackway 2009; Campbell et al. 2017). However, it is important to note that Australia’s rate of land clearing remains among the highest in the world (Bradshaw 2012; Evans 2016). With an ongoing net loss of habitat, restoration plantings are a critical conservation strategy for woodland birds and other fauna. Many restoration projects claim to focus on creating habitat for threatened and/or declining wildlife (e.g. Landcare Australia 2017). There is evidence that a focal-species approach can be used to develop guidelines for revegetation programs (Freudenberger 2001; Freudenberger and Brooker 2004; Wood et al. 2004). However, its usefulness as a conservation tool is debated (Lambeck 2002; Lindenmayer et al. 2002). Recent research suggests that although the focal-species approach has some merit, it is also necessary to ensure the flexibility of management actions such that all species are accounted for in conservation; focusing on one species may not benefit others of conservation concern, especially those which might not occur in species-rich assemblages (Lindenmayer et al. 2014). Furthermore, a generalised lack of information on the habitat requirements and population processes of many threatened and declining woodland bird species (Rayner et al. 2014) means that many revegetation programs are being implemented without sufficient knowledge as to the habitat requirements of the species they should be supporting (Block et al. 2001; Montague-Drake et al. 2009; Polyakov et al. 2015).

Reviews of restoration practice as early as the 1990s have outlined steps that should be taken to ensure the successful restoration of fragmented and degraded ecosystems, as well as challenges posed by large-scale revegetation (Pastorok et al. 1997; Block et al. 2001; Hobbs 2003; Lindenmayer et al. 2008; Duncan and Dorrrough 2009; Prober and Smith 2009; Campbell et al. 2017); also see the National Standards for the Practice of Ecological Restoration in Australia...
McDonald et al. 2016). The importance of setting measurable goals for restoration is crucial and underpins how we define long-term success in a restoration context (Cairns 2000; Block et al. 2001; Ruiz-Jaen and Aide 2005; Herrick et al. 2006; Hobbs 2017). This should include assessing the capacity of restoration plantings to support reproducing populations, an attribute that is rarely measured in restoration monitoring projects (Ruiz-Jaen and Aide 2005; Vesk and Mac Nally 2006).

Patterns: bird responses to revegetation in Australian temperate woodlands

Many pattern-based studies have investigated the effects of habitat loss, fragmentation and degradation on declining woodland bird species in Australia (reviewed by Ford et al. 2001; Ford 2011); fewer have examined how these species respond to restoration plantings (Nichols and Watkins 1984; Heath 2003; Robinson 2006; Lindenmayer et al. 2007; Barrett et al. 2008; Cunningham et al. 2008; Saunders and Nicholls 2008; Loyn et al. 2009; Selwood et al. 2009; Lindenmayer et al. 2010b; Munro et al. 2011; Shanahan et al. 2011; Lindenmayer et al. 2012; Bennett et al. 2013; Vesk et al. 2015). To date, much of the research on birds in revegetated landscapes has focused on answering the question ‘Do birds use restoration plantings?’, and concurrently, ‘Which plantings are preferentially selected?’

Previous research has discovered that some woodland bird species, including species of conservation concern, will readily occupy restoration plantings, and may even preferentially select plantings over remnant woodland (Nichols and Watkins 1984; Heath 2003; Kinross 2004; Martin et al. 2004; Kavanagh et al. 2007; Cunningham et al. 2008; Saunders and Nicholls 2008; Loyn et al. 2009; Lindenmayer et al. 2010b; Martin et al. 2011; Lindenmayer et al. 2012). These species have been termed ‘planting specialists’ – species that are more likely to be found in restoration plantings than in woodland remnants (Table 1). It should be noted that inferred habitat preferences for some species, such as the eastern yellow robin, scarlet robin, and southern whiteface (see Table 1 for scientific names), are not consistent among studies.

**TABLE 1**

Bird species occupancy and abundance in restoration plantings appears to be a complex relationship between context (location within the landscape, e.g. proximity to other areas of native vegetation), configuration (e.g. shape, area), and content (structural and floristic variables) (Nichols and Watkins 1984; Kavanagh et al. 2007; Cunningham et al. 2008; Kinross and Nicol 2008; Lindenmayer et al. 2010b; Munro et al. 2011; Lindenmayer et al. 2016) (Table 2). Differences in bird community composition in restoration plantings and remnant woodland have been consistently reported in...
Australia (Arnold 2003; Loyn et al. 2007; Martin et al. 2011; Munro et al. 2011; Lindenmayer et al. 2012), as well as in similarly restored habitat patches in Brazil (Becker et al. 2013), China (Zhang et al. 2011), Mexico (MacGregor-Fors et al. 2010), and the United States (Brawn 2006; Ortega-Álvarez et al. 2013). Some studies note that the bird community continually changes following initial establishment as planted vegetation matures and becomes more similar to remnant habitat (Lindenmayer et al. 2016; Debus et al. 2017); generalists and species favoured by open habitats are more common in the early stages, while shrub-dwelling and canopy specialists colonise as the habitat structure develops over time (Twedt et al. 2002; Heath 2003; Jansen 2005; Freeman et al. 2009; Gould and Mackey 2015).

Habitat composition and structure strongly influence bird community composition and abundance in restoration plantings (Arnold 2003; Barrett et al. 2008; Munro et al. 2011; Gould and Mackey 2015). In general, woodland bird abundance and diversity appears to increase with habitat complexity – the inclusion of a more diverse plant species assemblage, leaf litter, and an increase in canopy cover have all been positively associated with bird species richness and abundance (Barrett et al. 2008; Bonifacio et al. 2011; Munro et al. 2011; Gould and Mackey 2015). It is important to recognise the diverse ways in which different species or foraging guilds may respond to habitat features in restoration plantings. For example, Comer and Wooller (2002) found that a “clumped” spatial arrangement of shrubs in restoration plantings facilitated competitive exclusion of small honeyeaters by larger species, decreasing overall nectarivore diversity in the plantings. Barrett et al. (2008) found that ground-foraging insectivores were underrepresented in restoration plantings, and postulated that lack of native forb diversity may have been a likely cause. According to Arnold (2003), the inclusion of canopy and perching sites within one metre of the ground results in a greater abundance of insectivores in restoration plantings. Martin et al. (2004) found significantly lower abundances of species who primarily forage on bark in restoration plantings compared to woodland remnants; this may be due in part to the fact that certain habitat features, such as decorticating bark and fallen timber, take decades or even centuries to develop in temperate woodland habitats (Cunningham et al. 2007; Mac Nally 2008; Vesk et al. 2008; Munro et al. 2009). This may also be why restoration plantings are not predicted to support certain woodland-dependent bird species until 40, 60, or 100 years after establishment (Thomson et al. 2009).

There is evidence that the amount and proximity of remnant or planted vegetation in the area surrounding a restoration planting may have as much, if not more, influence on bird assemblage than the content of the planting itself (Kavanagh et al. 2007; Lindenmayer et al. 2007; 2010b). The rufous whistler (Pachycephala rufiventris) and grey fantail (Rhipidura albiscapa) are two species
that exhibit a positive response to an increase in the amount of planted native vegetation surrounding a restoration planting (Lindenmayer et al. 2010b). A habitat patch that is close to other patches may provide better foraging opportunities for species with large home ranges, such as the rufous whistler. Well-connected restoration plantings may also be key to supporting species whose local persistence is limited by dispersal, such as the brown treecreeper (Climacteris picumnus).

TABLE 2

**Process: breeding and persistence in restoration plantings**

Do restoration plantings actually provide suitable breeding habitat for woodland birds, and if they do, are attempts at breeding by birds in these sites successful? To persist in the long term, birds must be able to gain required resources from the patch they select (or from adjacent areas). This includes resources such as food and nesting sites, but also habitat services such as adequate protection from predation and competition (Figure 1).

FIGURE 1

There is documented evidence of breeding activity and site fidelity in multiple woodland bird species colonising young restoration plantings (2-3 years old) (Barrett et al. 2008). Bird breeding activity also has been reported in more mature plantings (up to 26 years old for directly planted sites, and 111 years for restored woodland remnants) (Selwood et al. 2009; Mac Nally et al. 2010; Bond 2011). However, species preference for, and occupancy of, a given habitat type is not necessarily correlated with long-term survival and persistence (Van Horne 1983; Battin 2004; Loyn et al. 2009). This is particularly relevant for declining species, which may occupy a site but display only limited evidence of successful breeding (Selwood et al. 2009; Mac Nally et al. 2010).

Restored habitats, including restoration plantings, have the potential to become ecological traps for bird populations. Ecological traps occur when individuals use habitat cues to preferentially colonise sites that are of inferior habitat quality and/or associated with lower breeding success than other sites (Kokko and Sutherland 2001; Schlaepfer et al. 2002; Battin 2004; Robertson and Hutto 2006). This concept differs from an ecological ‘sink’, which is simply an area of poor-quality habitat that is not preferentially occupied, in which the population tends toward decline (Dias 1996). Individuals may also inadvertently avoid high-quality patches due to misleading habitat cues, which likewise creates an ecological trap mechanism at the landscape level (Gilroy and Sutherland 2007). If restoration plantings were to act as ecological traps, with remnant habitat patches as the
population sources, metapopulation declines may be worsened rather than reversed by the extensive
planting of native vegetation (Figure 2).

FIGURE 2

There are some instances in the global literature of restored habitats acting as ecological traps. For
example, Larison et al. (2001) found that the song sparrow (Melospiza melodia) in restored riparian
forest in California had lower reproductive success than in naturally regenerating or mature forest,
due to the restored stands providing fewer nesting site choices and less protection from predation.
Managed prairie sites were described as ecological traps by Shochat et al. (2005), as higher
invertebrate abundances attracted breeding birds which subsequently experienced poorer nesting
success than in other sites. Chalfoun and Martin (2007) also documented lower nest success of
Brewer’s sparrow (Spizella breweri) in North American shrub-steppe landscapes with greater shrub
cover, despite greater densities of birds settling in these landscapes. Low-density populations, such
as those of many declining woodland bird species in Australia, face a high risk of local extinction in
ecological traps (Kokko and Sutherland 2001). Many Australian woodland birds are relatively long-
lived – 10-20 years is common in many species (Australian Bird and Bat Banding Scheme 2016).
Consequently, there may be a time-lag before the effects of a potential ecological trap mechanism
become apparent. It is therefore important to assess whether woodland birds are able to successfully
breed in restoration plantings. In the following sections, we discuss the primary factors likely to
influence the reproductive success of breeding birds in restoration plantings.

Nest predation

Predation is the primary driver of nest failure in most bird communities, causing up to 95% of failed
breeding attempts (Hanski et al. 1996; Zanette and Jenkins 2000; Guppy et al. 2017; Okada et al.
2017). Limited work has been done on the effects of predation on nest success in restoration
plantings internationally (Larison et al. 2001; Germaine and Germaine 2002), and no published
studies to date have sought to quantify nest predation or nest success in Australian temperate
woodland restoration plantings. Typical predation rates on the nests of birds vary greatly between
species, even for those with similar nest structures (Ford et al. 2001; Weidinger 2002). For
example, studies of the cup-nesting Australasian robins (Petroicidae) have consistently detected low
nest success rates – in the range of 10-47% – and identified nest predation as the most common
cause of failure (Robinson 1990; Zanette and Jenkins 2000; Armstrong et al. 2002; Debus 2006c).
Conversely, fantails (Rhipiduridae) typically have a 59-71% nest success rate, despite building cup-
nests that are less cryptic than those of robins (Cameron 1985). Parental behaviour, brood behaviour (e.g. begging), nest site choice and concealment, and habitat variables are among several factors that may interact and contribute to highly variable nest predation rates within and among bird communities (Martin et al. 2000; Haskell 2002; Weidinger 2002; Haff and Magrath 2011; Cancellieri and Murphy 2014). This variability is reflected in the diverse outcomes of nest predation studies (e.g. Zanette and Jenkins 2000; Debus 2006c; Guppy et al. 2017), and highlights the importance of conducting such studies in restoration plantings.

Nest predation is also fundamentally dependent on the type and abundance of predators in the vicinity of the nest (Muchai and du Plessis 2005; Guppy et al. 2017). Avian predators cause up to 96% of nest predation events in Australian forests and woodlands (Gardner 1998; Piper et al. 2002), and many predatory bird species, such as the pied currawong (Strepera graculina) and Australian magpie (Cracticus tibicen), have been favoured by habitat loss and fragmentation in temperate woodlands (Taylor and Ford 1998; Maron 2007). We might therefore expect to see higher rates of nest predation in restoration plantings in a fragmented landscape, where these species are more abundant, than in intact woodland remnants. Predator control may be an effective way of improving nest success in woodland birds (Debus 2006c), but is rarely undertaken – perhaps due to the considerable effort and resources required, in addition to the complex ecological and ethical considerations associated with controlling native predators (Wallach et al. 2010; 2015).

Patch size and isolation can interact with predation risk to influence breeding success and thus recruitment and persistence of birds in fragmented landscapes (reviewed by Stephens et al. 2004). Studies in fragmented landscapes worldwide have recorded lower breeding success and reproductive output in smaller habitat patches than in larger patches (Hoover et al. 1995; Burke and Nol 2000; Zanette and Jenkins 2000; Zanette 2001; Walk et al. 2010). These findings are frequently attributed to ‘edge-effects’, i.e. increased nest predation near habitat edges (Hoover et al. 1995; Burke and Nol 2000; Willson et al. 2001; Vander Haegen et al. 2002; Herkert et al. 2003; Wozna et al. 2017). However, this notion is challenged by other studies reporting no difference in nesting success or recruitment in smaller fragments (Lehnen and Rodewald 2009; Lollback et al. 2010; Walk et al. 2010) and/or no evidence of edge-effects increasing predator activity on nests (Hanski et al. 1996; Lahti 2001; Woodward et al. 2001; Piper et al. 2002; Boulton and Clarke 2003; Reino et al. 2010). It is important to consider the spatial scale of fragmentation relative to nest predation and its potential effects on bird populations – that is, whether fragmentation is occurring at the landscape, patch or edge scale (Zanette and Jenkins 2000; Stephens et al. 2004). Furthermore,
different predation processes, including different primary predators, may operate in fragmented
versus intact landscapes (Vander Haegen et al. 2002).

The contrasting outcomes of studies of nest success in fragmented landscapes imply that the effects
of influential processes are either species-specific or landscape-dependent or both. In general, we
might expect species that typically experience high levels of nest predation to experience greater
nest success in larger restoration plantings, or in plantings surrounded by a greater amount of
vegetation cover. However, surrounding land-use may have unexpected effects on the distribution
and abundance of nest predators and thus nesting success, irrespective of patch size or connectivity.
Indeed, a recent study by Okada et al. (2017) found effects of both nest type and the surrounding
matrix (i.e. land use) on breeding success of small-bodied woodland birds in a fragmented
landscape. The results were contrary to expectations – nesting success for dome-nesting species was
higher in woodland patches surrounded by grazing land than patches surrounded by pine
plantations, with abundance of avian predator nests thought to be a contributing factor. Monitoring
nest predation and success is an under-utilised pathway to understanding which species are being
supported in the long term, and enabling management decisions to tailor restoration programs for
species more vulnerable to predation. These topics should be thoroughly investigated in future
research.

Nest site selection

The importance of nest site microhabitat selection in bird breeding success has been documented
both internationally (Martin 1998; Mezquida 2004; Smith et al. 2009; Schlossberg and King 2010;
Murray and Best 2014) and in Australia (Oliver et al. 1998; Cousin 2009; Soanes et al. 2015).
However, research concerning woodland species nesting in restoration plantings is lacking, and may
be a critical determinant of breeding success (Martin 1998). This is particularly relevant for species
vulnerable to predation, such as cup-nesters (Okada et al. 2017). Nest-site selection for such species
may act as a stronger selective pressure than other variables. For example, the western yellow robin
(Eopsaltria griseogularis) favours sites with views of the nest surroundings over foraging
opportunities when selecting a nest site (Cousin 2009), indicating that predation is a primary
concern for nesting individuals of this species. It is crucial that restoration plantings provide
suitable nesting sites for a range of woodland bird species, lest they fail to support breeding
populations (Larison et al. 2001). For example, the inclusion of trees with dense and/or pendulous
foliage may increase availability of well-concealed nesting sites for foliage-nesters such as the
weebill and yellow thornbill. Species that nest in lower strata, such as the superb fairy-wren and
speckled warbler, may be better supported with the presence of native grasses and/or the
accumulation of dead woody material and leaf litter in the ground layer. These are factors rarely
considered when constructing or monitoring restoration plantings.

Resource availability

Resource distribution and abundance in habitat patches are critical determinants of woodland bird
site occupancy and foraging patterns (Gilmore 1986; Barrett et al. 2008; Vesker et al. 2008;
Montague-Drake et al. 2009; Munro et al. 2011). For example, litter and bare ground are important
habitat features supporting ground-foraging birds such as robins and thornbills (Bromham et al.
1999; Antos and Bennett 2006). Species in these groups also prefer a low density of shrubs, as does
the diamond firetail (Antos et al. 2008). Other species may rely on various other resources, such as
woody debris – reintroduced brown treecreepers in a vegetation reserve responded positively only
when woody debris was included as a habitat feature (Bennett et al. 2013). A lack of woody debris
may be one reason the brown treecreeper is currently underrepresented in restoration plantings
(Martin et al. 2004; 2011; Lindenmayer et al. 2012; Gould and Mackey 2015). Furthermore,
woodland bird species, including the brown treecreeper and southern whiteface, are known to vary
their foraging habits and use of foraging substrates between the breeding and non-breeding seasons
(Antos and Bennett 2006). This highlights the importance of using prior knowledge of species’
habitat requirements to inform predicted responses of birds to habitat restoration (Bennett et al.
2013).

Food is generally considered a limiting resource for breeding birds (von Brömssen and Jansson
1980; Hochachka and Boag 1987; Simons and Martin 1990; Verhulst 1994; Granbom and Smith
2006; Wellicome et al. 2013). However, the addition of food resources does not tend to prevent
major declines in fluctuating populations of terrestrial vertebrates (Boutin 1990), suggesting that the
mechanisms of species decline are not usually related to resource-limitation alone. Nonetheless, it is
vital to assess the role of food resources in woodland bird habitat suitability. The study by Zanette
et al. (2000) is unique in its exploration of food shortage affecting birds in fragmented Australian
woodlands; the authors documented lower availability of food resources in smaller versus larger
fragments, with breeding success found to be lower in smaller fragments. Restoration plantings
overwhelmingly comprise small habitat patches (Freudenberger et al. 2004; Smith 2008), and are
known to attract a variety of bird species, including species of conservation concern (Lindenmayer
et al. 2010b). When colonising sites, birds are motivated by habitat cues indicative of high resource
availability, such as vegetation structure (Kokko and Sutherland 2001). If resource availability in
restoration plantings does not accurately reflect these cues, then there is an increased likelihood of
ecological trap mechanisms operating in revegetated landscapes (Schlaepfer et al. 2002).
Home range sizes of birds are inversely related to resource density and resource renewal rates (Ford 1983). This means that larger home ranges are required in habitats with fewer available resources. In a fragmented landscape, birds that are unwilling to cross habitat gaps may be disadvantaged if they are unable to expand their home ranges to exploit resources in adjacent patches (Fahrig 2007; Robertson and Radford 2009). Patchily distributed or scarce food resources can lead to inefficient foraging patterns, with subsequent reduced fitness and reproductive output in birds (Pyke 1984; Martin 1987; Granbom and Smith 2006; Flockhart et al. 2016). In the breeding season, optimal central place foraging (i.e. the need to regularly return to the nest) influences searching movements, distance travelled, and prey selection (Pyke 1984). In a fragmented landscape, the need to expand foraging areas or depart a patch due to resource depletion can measurably increase energy expenditure for breeding birds, thus reducing their reproductive fitness. For example, birds in fragmented landscapes may spend up to 64% more energy per chick raised than those breeding in intact remnant woodland (Hinsley et al. 2008). Small woodland patches have also been associated with the contraction of breeding seasons, eggs of lighter mass being laid, and smaller nestlings being produced (Zanette et al. 2000). These issues could influence the breeding success of birds in restoration plantings.

For insectivorous birds in particular, dietary composition and hence dietary quality is directly related to habitat quality (Razeng and Watson 2012). Terrestrial invertebrates can display strong responses to habitat variables in fragmented temperate woodlands (Bromham et al. 1999; Barton et al. 2009; Lindsay and Cunningham 2009; Gibb and Cunningham 2010). As an example, Zanette et al. (2000) identified a 50% lower biomass of surface-dwelling invertebrates in small (55 ha) relative to large (>400 ha) woodland fragments, thereby linking food resources for insectivorous birds to patch size. Coleoptera constitute the largest proportion of prey items for declining insectivorous woodland birds, followed by Formicidae and Lepidoptera (Razeng and Watson 2012). Coleoptera and other preferred prey of insectivorous birds have been shown to respond positively to some restoration treatments (e.g. removal of grazing pressure, addition of fallen logs to habitat patches) (Lindsay and Cunningham 2009; Gibb and Cunningham 2010). However, there is also evidence that restoration plantings may not help restore invertebrate communities in agricultural landscapes (Jellinek et al. 2013). It is important to understand and consider the effects of habitat fragmentation and restoration on invertebrate prey of woodland birds when assessing habitat quality in restoration plantings.
Competition

Interspecific competition for resources is a strong selective process that is enhanced in habitats with depleted or patchy resources (Cody 1981). Sought-after resources such as food and nesting sites are defended by birds in established territories, especially during the breeding season (Robinson 1989; Broughton et al. 2012; Belder 2013). Closely-related species may compete for similar resources, particularly food. For example, Robinson (1990) found that flame robins and scarlet robins compete more for food resources than nest sites. The noisy miner (Manorina melanocephala) is a strong competitor for territories and resources in Australian temperate woodlands, and actively disrupts and excludes other small woodland birds (Grey et al. 1998; Maron 2007; Montague-Drake et al. 2011; Maron et al. 2013; Bennett et al. 2015). Competition from the noisy miner has been shown to decrease breeding activity in species of smaller body mass, and can have a greater influence on woodland bird distribution and recruitment than vegetation characteristics (Bennett et al. 2015; Mortelliti et al. 2016). Recent research has revealed that the noisy miner is both increasing the risk of woodland birds going extinct from habitat patches, and decreasing the chances of them colonising patches (Mortelliti et al. 2016). The composition of restoration plantings can significantly affect the likelihood of colonisation and occupancy by the noisy miner; inclusion of a Eucalyptus overstorey increases the likelihood of noisy miner colonisation as the vegetation matures (Maron 2007). Conversely, the inclusion of an Acacia understorey reduces noisy miner occupancy (Lindenmayer et al. 2010b). Monitoring restoration plantings for factors likely to increase competition and competitive exclusion will provide a better understanding of species persistence mechanisms in these environments.

Brood parasitism

The influence of brood parasitism on nest success is a factor often discussed in international studies of habitat restoration (Delpey and Dinsmore 1993; Fletcher et al. 2006; Small et al. 2007; Forrester 2015), but limited research has been done on this topic in Australian temperate woodland ecosystems (Ford 2011) – but see Guppy et al. (2017). There is evidence suggesting that parasitic cuckoos are dependent on large woodland remnants with an abundance of their preferred host species, and that host species may experience greater breeding success in smaller fragments where cuckoos are rare (Brooker and Brooker 2003). Restoration plantings typically create small habitat patches (Freudenberger et al. 2004; Smith 2008), thus brood parasitism events may be infrequent in revegetated sites. However, to our knowledge, no empirical studies to date have documented brood parasitism in temperate woodland restoration plantings, so its potential effect on the reproductive success of woodland birds in revegetated landscapes remains unknown.
Summary and future research directions

Research to date has shown that the responses of woodland birds to revegetation are varied, and while the habitat requirements of some species may be met, there is still much to learn about the long-term responses of birds to landscape-scale habitat restoration. Ostensibly, occupancy data alone may not expose underlying trends in population processes, or drivers of breeding success and site fidelity. To prevent and reverse the ongoing decline of Australia’s woodland avifauna, and re-establish endangered habitat in highly fragmented agricultural landscapes, it is vital that temperate woodland restoration efforts continue and increase over the coming years. However, to ensure that restoration plantings are both an ecologically-effective and cost-effective biodiversity conservation strategy, it is also essential for their design and management to be informed by scientific research.

There is an increasing number of modelling studies proposing strategies for optimising landscape restoration, aiming to solve the issues of catering for multiple species and ensuring maximum cost-effectiveness in the face of limited conservation resources (Bennett and Mac Nally 2004; Holzkämper et al. 2006; Thomson et al. 2007; Westphal et al. 2007; Thomson et al. 2009; Lethbridge et al. 2010; McBride et al. 2010; Huth and Possingham 2011; Polyakov et al. 2015; Ikin et al. 2016). Many of these studies provide information to help guide future restoration efforts in Australia. However, because conservation and restoration remain low priorities for governments, almost all the proposed strategies are yet to be empirically tested. Furthermore, to the best of our knowledge, all such studies are based on pattern data. Due to the lack of knowledge on population processes in revegetated landscapes, optimisation strategies for restoration to support breeding populations of woodland birds are non-existent.

Developing a comprehensive understanding of woodland bird ecology in revegetated landscapes is fundamental to devising knowledge-based solutions to reverse species decline (Bennett and Watson 2011), and a necessary key step is to move beyond pattern data towards quantifying population responses of birds to habitat restoration. We suggest that future research in restoration plantings should focus on the areas of interest and knowledge gaps identified by this review (summarised in Table 3), with an emphasis on exploring factors at the landscape- and patch-scale that are likely to contribute to restoration plantings acting as ecological traps. In particular, based on our review, we suggest the following questions should be addressed as priorities:

- What cues do birds use to select habitat in revegetated landscapes?
- Are woodland birds resident in restoration plantings in the long term?
- Do restoration plantings have higher immigration and/or mortality rates than woodland remnants?
Is habitat quality in restoration plantings sufficient for woodland birds to breed successfully?

Does habitat suitability for breeding birds change over time as plantings mature?

How does the breeding success of birds in plantings compare to that of birds in remnant woodland?

What are the primary nest predators and rates of nest failure due to predation?

Do restoration plantings provide suitable nesting sites and adequate food resources for woodland birds?

What is the role of competitive exclusion by the noisy miner?

What is the role of brood parasitism in restoration plantings?

Finally, a more thorough approach to monitoring restored habitats is required to determine their ability to support breeding populations of woodland birds. As Battin (2004) emphasised, ‘…we cannot afford to ignore the possibility of ecological traps or fail to take them into account in the study, management, and conservation of animal populations.’ Crucially, the capacity to accurately evaluate the success of restoration plantings in achieving intended conservation goals underpins effective utilisation of conservation resources, as well as ecologically sound environmental management.

**TABLE 3**

**Acknowledgements**

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Figure 1 Conceptual diagram of interrelated factors that may influence the breeding success and persistence of woodland bird populations in restoration plantings. Bold/double rectangles = the processes we focus on in this review (breeding success and persistence). Rounded rectangles = population processes i.e. what the birds are doing. Rectangles = broad patch-level characteristics i.e. what type of habitat the birds are living in and where. Circles = fine-scale patch-level attributes i.e. what the birds experience in the habitat patch.
Figure 2 A conceptual model of an ecological trap mechanism operating in a fragmented landscape with restoration plantings and remnant patches. Restoration plantings have the potential to become ecological traps if they are preferentially occupied but lead to lower reproductive success and/or higher mortality than remnant patches. ○ = population process, △ = trend in population process, □ = habitat type.
Table 1 – Planting specialists

Woodland bird species identified as ‘planting specialists’ – bird species more likely to be found in plantings than in remnants or other sites – in Australian studies of bird occurrence, distribution and abundance in revegetated landscapes. Species are listed in taxonomic order (Christidis and Boles 2008).

<table>
<thead>
<tr>
<th>Species</th>
<th>Studies</th>
<th>Study region(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>superb fairy-wren</td>
<td>Malurus cyaneus</td>
<td>Barrett et al. 2008;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Cunningham et al. 2008;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Martin et al. 2011;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lindenmayer et al. 2012</td>
</tr>
<tr>
<td>white-browed scrubwren</td>
<td>Sericornis frontalis</td>
<td>Cunningham et al. 2008</td>
</tr>
<tr>
<td>speckled warbler&lt;sup&gt;C&lt;/sup&gt;</td>
<td>Chthonicola sagittata</td>
<td>Kavanagh et al. 2007;</td>
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<tr>
<td></td>
<td></td>
<td>Cunningham et al. 2008</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lindenmayer et al. 2012</td>
</tr>
<tr>
<td>weebill&lt;sup&gt;C&lt;/sup&gt;</td>
<td>Smicromis brevirostris</td>
<td>Kavanagh et al. 2007;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Cunningham et al. 2008;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Martin et al. 2011</td>
</tr>
<tr>
<td>western gerygone</td>
<td>Gerygone fusca</td>
<td>Cunningham et al. 2008;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lindenmayer et al. 2012</td>
</tr>
<tr>
<td>striated thornbill</td>
<td>Acanthiza lineata</td>
<td>Kavanagh et al. 2007</td>
</tr>
<tr>
<td>yellow thornbill</td>
<td>Acanthiza nana</td>
<td>Kavanagh et al. 2007;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Cunningham et al. 2008;</td>
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<tr>
<td></td>
<td></td>
<td>Martin et al. 2011;</td>
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<tr>
<td></td>
<td></td>
<td>Lindenmayer et al. 2012</td>
</tr>
<tr>
<td>yellow-rumped thornbill&lt;sup&gt;C&lt;/sup&gt;</td>
<td>Acanthiza chrysorrhoa</td>
<td>Cunningham et al. 2008;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Martin et al. 2011;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lindenmayer et al. 2012</td>
</tr>
<tr>
<td>southern whiteface&lt;sup&gt;C&lt;/sup&gt;</td>
<td>Aphelocephala leucopsis</td>
<td>Barrett et al. 2008;</td>
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<td>white-plumed honeyeater</td>
<td>Lichenostomus penicillatus</td>
<td>Barrett et al. 2008;</td>
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<td>Martin et al. 2011;</td>
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<td></td>
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<td>Lindenmayer et al. 2012</td>
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<tr>
<td>red wattlebird</td>
<td>Anthochaera carunculata</td>
<td>Cunningham et al. 2008;</td>
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<td></td>
<td>Lindenmayer et al. 2012</td>
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<td>rufous whistler&lt;sup&gt;C&lt;/sup&gt;</td>
<td>Pachycephala rufiventris</td>
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<td>grey strike-thrush</td>
<td>Colluricincla harmonica</td>
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<td>Rhipidura albiscapa</td>
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<td>willie wagtail</td>
<td>Rhipidura leucophrys</td>
<td>Heath 2003; Martin et al. 2011; Lindenmayer et al. 2012</td>
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<td>scarlet robin&lt;sup&gt;CV&lt;/sup&gt;</td>
<td>Petroica boodang</td>
<td>Cunningham et al. 2008</td>
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<tr>
<td>red-capped robin&lt;sup&gt;C&lt;/sup&gt;</td>
<td>Petroica goodenovii</td>
<td>Cunningham et al. 2008;</td>
</tr>
<tr>
<td>flame robin&lt;sup&gt;CV&lt;/sup&gt;</td>
<td>Petroica phoenicea</td>
<td>Lindenmayer et al. 2012</td>
</tr>
<tr>
<td>hooded robin&lt;sup&gt;CV&lt;/sup&gt;</td>
<td>Melanodryas cucullata</td>
<td>Cunningham et al. 2008</td>
</tr>
<tr>
<td>eastern yellow robin</td>
<td>Eopsaltria australis</td>
<td>Cunningham et al. 2008</td>
</tr>
<tr>
<td>red-browed finch</td>
<td>Neochmia temporalis</td>
<td>Kavanagh et al. 2007;</td>
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<td>Barrett et al. 2008;</td>
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<td></td>
<td></td>
<td>Cunningham et al. 2008;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lindenmayer et al. 2012</td>
</tr>
<tr>
<td>diamond firetail&lt;sup&gt;CV&lt;/sup&gt;</td>
<td>Stagonopleura guttata</td>
<td>Cunningham et al. 2008</td>
</tr>
</tbody>
</table>

<sup>C</sup> Of conservation concern
<sup>V</sup> Classified as Vulnerable in NSW
Table 2 – Restoration planting characteristics and woodland bird occupancy

Variables found to influence occupancy by bird species in restoration plantings in Australian studies of bird occurrence, distribution and abundance in revegetated landscapes. Adapted from Lindenmayer et al. (2010b).

<table>
<thead>
<tr>
<th>Variable type</th>
<th>Variable</th>
<th>Studies</th>
<th>Study region(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Context</strong></td>
<td>Landscape vegetation cover, distance to nearest other native vegetation</td>
<td>Heath 2003; Barrett et al. 2008; Selwood et al. 2009; Lindenmayer et al. 2010b; Munro et al. 2011</td>
<td>Goomalling Shire, WA; Box-ironbark region, VIC; South-west Slopes, NSW; West Gippsland, VIC</td>
</tr>
<tr>
<td><strong>Configuration</strong></td>
<td>Shape</td>
<td>Lindenmayer et al. 2010b</td>
<td>South-west Slopes, NSW</td>
</tr>
<tr>
<td></td>
<td>Area</td>
<td>Selwood et al. 2009; Lindenmayer et al. 2010b; Munro et al. 2011</td>
<td>Box-ironbark region, VIC; South-west Slopes, NSW; West Gippsland, VIC</td>
</tr>
<tr>
<td></td>
<td>Topography</td>
<td>Lindenmayer et al. 2010b</td>
<td>South-west Slopes, NSW</td>
</tr>
<tr>
<td><strong>Content</strong></td>
<td>No. plants</td>
<td>Lindenmayer et al. 2010b</td>
<td>South-west Slopes, NSW</td>
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<tr>
<td></td>
<td>No. native plant species</td>
<td>Barrett et al. 2008; Munro et al. 2011</td>
<td>South-west Slopes, NSW; West Gippsland, VIC</td>
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<tr>
<td></td>
<td>Canopy depth</td>
<td>Lindenmayer et al. 2010b</td>
<td>South-west Slopes, NSW</td>
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<td>Canopy height</td>
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<td>Overstorey cover</td>
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<td>Midstorey cover</td>
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<td></td>
<td>Understorey/ground cover</td>
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<td>Goomalling Shire, WA; Wandoo woodland, WA; South-west Slopes, NSW</td>
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<td></td>
<td>Mistletoe</td>
<td>Lindenmayer et al. 2010b</td>
<td>South-west Slopes, NSW</td>
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<tr>
<td></td>
<td>Logs, fallen timber, leaf litter</td>
<td>Barrett et al. 2008; Selwood et al. 2009; Lindenmayer et al. 2010b; Munro et al. 2011</td>
<td>Box-ironbark region, VIC; South-west Slopes, NSW; West Gippsland, VIC</td>
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<tr>
<td></td>
<td>Dead trees/shrubs</td>
<td>Lindenmayer et al. 2010b</td>
<td>South-west Slopes, NSW</td>
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<td></td>
<td>Remnant/paddock trees</td>
<td>Selwood et al. 2009; Lindenmayer et al. 2010b; Munro et al. 2011</td>
<td>Box-ironbark region, VIC; South-west Slopes, NSW; West Gippsland, VIC</td>
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<tr>
<td></td>
<td>Grazing</td>
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<td>Box-ironbark region, VIC; South-west Slopes, NSW</td>
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<tr>
<td></td>
<td>Age</td>
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<tr>
<td></td>
<td>Vegetation condition</td>
<td>Munro et al. 2011</td>
<td>West Gippsland, VIC</td>
</tr>
</tbody>
</table>
### Table 3 – Future research directions

Summary of past and present research on birds in fragmented agricultural landscapes and landscapes undergoing habitat restoration, with recommended future research directions.

<table>
<thead>
<tr>
<th>Key area</th>
<th>Early work Topic</th>
<th>Conclusions</th>
<th>Present focus Topic</th>
<th>Conclusions</th>
<th>Future directions</th>
</tr>
</thead>
</table>
| Distribution and abundance| Occupancy of restoration plantings by woodland birds (e.g. Munro et al. 2011; Lindenmayer et al. 2010) | (i) Woodland bird species, including species of conservation concern, occupy restoration plantings  
(ii) Restoration plantings and remnant sites support different bird communities | Role of restoration plantings as habitat for woodland birds in a landscape context (e.g. Mortelliti et al. 2016) | Restoration plantings may not act as habitat refuges for woodland birds, including species of conservation concern | Factors influencing habitat selection by woodland birds in fragmented agricultural landscapes |
| Population dynamics       | Ecological traps (e.g. Battin 2004)                                              | Importance of understanding interactions between habitat selection and habitat quality | Ecological traps and undervalued resources (e.g. Gilroy and Sutherland 2007)           | Understanding factors that influence colonisation of high-quality sites can inform management decisions | Quantifying habitat quality in restoration plantings; identifying potential ecological trap mechanisms in revegetated landscapes |
| Resources                 | Food resources in woodland fragments (e.g. Zanette et al. 2000)                  | Food resource availability lower in smaller than in larger woodland fragments | Resources in restored landscapes (e.g. Le Roux et al. 2016)                           | Restoration plantings may take decades to develop habitat features of remnant sites, such as nest hollows | Resource availability (food and nesting sites) in restoration plantings |
|                          | Conservation of Coleoptera assemblages closely linked to microhabitat variables e.g. fallen logs | Coleoptera assemblages may show either positive or neutral responses to habitat restoration | Coleoptera assemblages may show either positive or neutral responses to habitat restoration | Coleoptera assemblages may show either positive or neutral responses to habitat restoration | Coleoptera assemblages may show either positive or neutral responses to habitat restoration |
| Breeding success          | Nesting ecology of woodland birds (e.g. Robinson 1990)                          | Nest failures mostly due to predation                                        | Bird breeding success in restoration plantings (e.g. Mac Nally et al. 2010)          | Little evidence of successful breeding in restoration plantings                | Quantifying nest success in restoration plantings, identifying causes of success/failure |
|                          | Confliction results: nest predation may be same in small and large fragments, or increased by edge-effects in small fragments | Role of nest predation in woodland bird species declines (e.g. Debus 2006)     | Role of nest predation in woodland bird species declines (e.g. Debus 2006)          | Intense nest predation likely cause of decline for woodland bird species of conservation concern | Quantifying nest predation, identifying primary nest predators in restoration plantings |
| Species interactions      | Nest predation in small patches (e.g. Zanette and Jenkins 2000; Vander Haegen et al. 2002) | Brood parasites by brown-headed cowbirds (Molothrus ater) lower in restored than in remnant landscapes | Brood parasitism in Australian temperate woodlands                                   | Horsfield’s bronze-cuckoo (Chalcites basalis) may be dependent on large habitat fragments | Brood parasitism in temperate woodland restoration plantings |
|                          | Influence of noisy miner on woodland bird communities (e.g. Grey et al. 1998)    | Influence of noisy miner on landscape-level bird species distribution patterns (e.g. Mortelliti et al. 2016) | Influence of noisy miner on landscape-level bird species distribution patterns (e.g. Mortelliti et al. 2016) | Noisy miner main driver of bird distribution patterns in fragmented woodlands, prevents restoration plantings acting as habitat refuges | Effects of noisy miner removal on landscape-level bird species distribution patterns and restoration plantings occupation |

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