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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 2007; Duncan and Dorrough 2009; Mac Nally *et al.* 2009; Prober *et al.* 2012; 2014).

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 Dorrough 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 cupnests 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; Vesk *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 (Delphey 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

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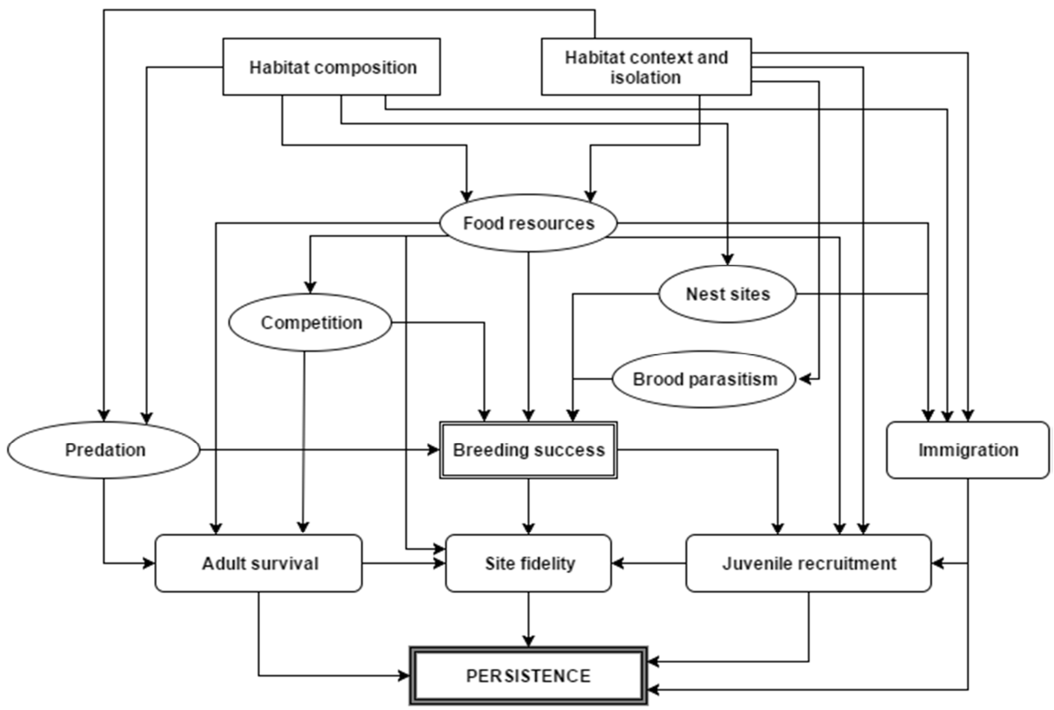

Figure 1 Conceptual diagram of interrelated factors that may influence the breeding success and persistence of woodland bird populations in restoration plantings. Bold/double rectangles = the processes we focus on in this review (breeding success and persistence). Rounded rectangles = population processes 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.

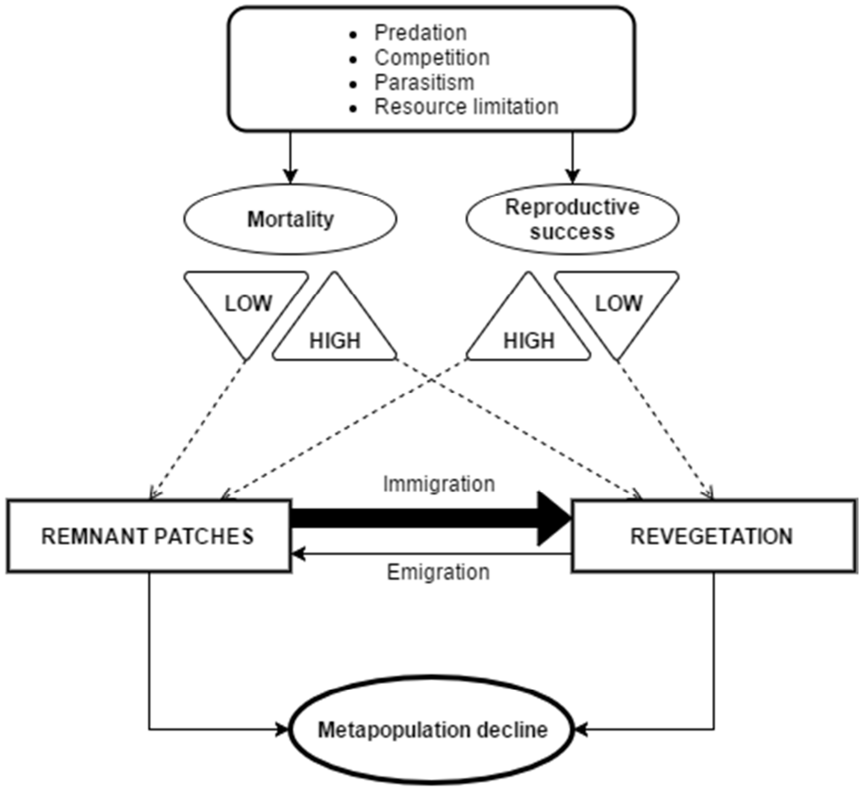

Figure 2 A conceptual model of an ecological trap mechanism operating in a fragmented landscape with restoration plantings and remnant patches. Restoration plantings have the potential to become ecological traps if they are preferentially occupied but lead to lower reproductive success and/or higher 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).

Species		Studies	Study region(s)
superb fairy-wren	*Malurus cyaneus*	Barrett *et al.* 2008; Cunningham *et al.* 2008; Martin *et al.* 2011; Lindenmayer *et al.* 2012	South-west Slopes, NSW
white-browed scrubwren	*Sericornis frontalis*	Cunningham *et al.* 2008	South-west Slopes, NSW
speckled warbler[C]	*Chthonicola sagittata*	Kavanagh *et al.* 2007; Cunningham *et al.* 2008; Lindenmayer *et al.* 2012	South-west Slopes, NSW
weebill[C]	*Smicrornis brevirostris*	Kavanagh *et al.* 2007; Cunningham *et al.* 2008; Martin *et al.* 2011	South-west Slopes, NSW
western gerygone	*Gerygone fusca*	Cunningham *et al.* 2008; Lindenmayer *et al.* 2012	South-west Slopes, NSW
striated thornbill	*Acanthiza lineata*	Kavanagh *et al.* 2007	South-west Slopes, NSW
yellow thornbill	*Acanthiza nana*	Kavanagh *et al.* 2007; Cunningham *et al.* 2008; Martin *et al.* 2011; Lindenmayer *et al.* 2012	South-west Slopes, NSW
yellow-rumped thornbill[C]	*Acanthiza chrysorrhoa*	Cunningham *et al.* 2008; Martin *et al.* 2011; Lindenmayer *et al.* 2012	South-west Slopes, NSW
southern whiteface[C]	*Aphelocephala leucopsis*	Barrett *et al.* 2008;	South-west Slopes, NSW
white-plumed honeyeater	*Lichenostomus penicillatus*	Barrett *et al.* 2008; Martin *et al.* 2011; Lindenmayer *et al.* 2012	South-west Slopes, NSW
red wattlebird	*Anthochaera carunculata*	Cunningham *et al.* 2008; Lindenmayer *et al.* 2012	South-west Slopes, NSW
rufous whistler[C]	*Pachycephala rufiventris*	Kavanagh *et al.* 2007; Lindenmayer *et al.* 2012	South-west Slopes, NSW
grey shrike-thrush	*Colluricincla harmonica*	Martin *et al.* 2011; Lindenmayer *et al.* 2012	South-west Slopes, NSW
grey fantail	*Rhipidura albiscapa*	Cunningham *et al.* 2008; Lindenmayer *et al.* 2012	South-west Slopes, NSW
willie wagtail	*Rhipidura leucophrys*	Heath 2003; Martin *et al.* 2011; Lindenmayer *et al.* 2012	Goomalling Shire, WA; South-west Slopes, NSW
scarlet robin[CV]	*Petroica boodang*	Cunningham *et al.* 2008	South-west Slopes, NSW
red-capped robin[C]	*Petroica goodenovii*	Cunningham *et al.* 2008; Lindenmayer *et al.* 2012	South-west Slopes, NSW
flame robin[CV]	*Petroica phoenicea*	Lindenmayer *et al.* 2012	South-west Slopes, NSW
hooded robin[CV]	*Melanodryas cucullata*	Cunningham *et al.* 2008	South-west Slopes, NSW
eastern yellow robin	*Eopsaltria australis*	Cunningham *et al.* 2008	South-west Slopes, NSW
red-browed finch	*Neochmia temporalis*	Kavanagh *et al.* 2007; Barrett *et al.* 2008; Cunningham *et al.* 2008; Lindenmayer *et al.* 2012	South-west Slopes, NSW
diamond firetail[CV]	*Stagonopleura guttata*	Cunningham *et al.* 2008	South-west Slopes, NSW

[C] Of conservation concern
[V] 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).

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

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.

Key area	Early work		Present focus		Future directions
	Topic	Conclusions	Topic	Conclusions	Topic
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 invertebrates in woodland remnants (e.g. Barton *et al.* 2009)	Coleoptera assemblage composition closely linked to microhabitat variables e.g. fallen logs	Invertebrate community responses to habitat restoration (e.g. Gibb and Cunningham 2010; Jellinek *et al.* 2013)	Coleoptera assemblages may show either positive or neutral responses to habitat restoration	Responses of invertebrate prey of woodland birds to 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
Species interactions	Nest predation in small patches (e.g. Zanette and Jenkins 2000; Vander Haegen *et al.* 2002)	Conflicting 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)	Intense nest predation likely cause of decline for woodland bird species of conservation concern	Quantifying nest predation, identifying primary nest predators in restoration plantings
	Brood parasitism in North American landscapes (e.g. Larison *et al.* 2001)	Brood parasitism 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)	Noisy miner disrupts and excludes small insectivorous birds from habitat patches in fragmented landscapes	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 planting occupancy