

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

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Complete List of Authors:	Belder, Donna; Fenner School of Environment and Society, The Australian National University; National Environmental Science Program Threatened Species Recovery Hub, The Australian National University Pierson, Jennifer; Fenner School of Environment and Society, The Australian National University; Environment, Planning and Sustainable Development Directorate, ACT Government Ikin, Karen; Fenner School of Environment and Society, The Australian National University; National Environmental Science Program Threatened Species Recovery Hub, The Australian National University; ARC Centre of Excellence for Environmental Decisions, The Australian National University Lindenmayer, David; Australian National University, Fenner School of Environment and Society; National Environmental Science Program Threatened Species Recovery Hub, The Australian National University; ARC Centre of Excellence for Environmental Decisions, The Australian National University; ARC
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2 conservation of woodland birds through restoration plantings

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- 4 Donna J. Belder A B E
- 5 Jennifer C. Pierson^{AC}
- 6 Karen Ikin^{ABD}
- 7 David B. Lindenmayer A B D
- 8

9 ^A Fenner School of Environment and Society, The Australian National University, Canberra, ACT,

10 2601 Australia

¹¹ ^B National Environmental Science Program Threatened Species Recovery Hub, The Australian

12 National University, Canberra, ACT, 2601 Australia

13 ^C Environment, Planning and Sustainable Development Directorate, ACT Government, Canberra,

- 14 ACT, 2620 Australia
- ¹⁵ ARC Centre of Excellence for Environmental Decisions, The Australian National University,
- 16 Canberra, ACT, 2601 Australia

17 ^E Corresponding author. Email: <u>donna.belder@anu.edu.au</u>

18

19 Abstract

20 Habitat loss due to land conversion for agriculture is a leading cause of global biodiversity loss and 21 altered ecosystem processes. Restoration plantings are an increasingly common strategy to address 22 habitat loss in fragmented agricultural landscapes. However, the capacity of restoration plantings to 23 support reproducing populations of native plants and animals is rarely measured or monitored. This 24 review focuses on avifaunal response to revegetation in Australian temperate woodlands - one of 25 the world's most heavily altered biomes. Woodland birds are a species assemblage of conservation 26 concern, but only limited research to date has gone beyond pattern data and occupancy trends to 27 examine whether they persist and breed in restoration plantings. Moreover, habitat quality and 28 resource availability, including food, nesting sites, and adequate protection from predation, remain 29 largely unquantified. Several studies have found that some bird species, including species of 30 conservation concern, will preferentially occupy restoration plantings relative to remnant woodland 31 patches. However, detailed empirical research to verify long-term population growth, colonisation 32 and extinction dynamics is lacking. If restoration plantings are preferentially occupied but fail to 33 provide sufficient quality habitat for woodland birds to form breeding populations, they may act as

34 ecological traps, exacerbating population declines. Monitoring breeding success and site fidelity are 35 under-utilised pathways to understanding which, if any, bird species are being supported by 36 restoration plantings in the long term. There has been limited research on these topics 37 internationally, and almost none in Australian temperate woodland systems. Key knowledge gaps 38 centre on provision of food resources, formation of optimal foraging patterns, nest predation levels 39 and the prevalence of primary predators, the role of brood parasitism, and the effects of patch size 40 and isolation on resource availability and population dynamics in a restoration context. To ensure 41 that future restoration plantings benefit woodland birds and are cost-effective as conservation 42 strategies, the knowledge gaps identified by this review should be investigated as priorities in future 43 research.

44 Introduction

45 A large fraction of the world's woodland and forest avifauna is declining (IUCN 2016; Waldron et 46 al. 2017), reflecting the well-documented global trend of biodiversity loss associated with 47 intensifying anthropogenic activities (Butchart et al. 2010). An increasingly common strategy to 48 address habitat loss in fragmented agricultural landscapes is the creation of habitat through 49 revegetation, often referred to as "restoration plantings" (Pastorok et al. 1997; Cairns 2000; Rey 50 Benayas et al. 2009; Barral et al. 2015). These are typically small patches of planted native 51 vegetation, and are often intended to facilitate landscape connectivity and conservation of fauna 52 such as birds (Block et al. 2001; Freudenberger 2001). Patterns of bird species occupancy and 53 abundance in restoration plantings are commonly used to infer habitat quality (Cunningham et al. 54 2008; Munro et al. 2011; Lindenmayer et al. 2012). However, there has been limited research on 55 the population responses of birds to restoration plantings or other forms of habitat restoration, such 56 as remediation (Larison *et al.* 2001; Germaine and Germaine 2002). It is crucial to understand the 57 population dynamics of birds in revegetated landscapes to establish whether restoration plantings 58 provide quality habitat in which birds can survive and reproduce. This is particularly relevant for 59 threatened and declining bird assemblages that may come to rely on restoration plantings for long-60 term population stability.

61

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

67 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

69 fundamental to determine the conservation and management value of restoration plantings,

70 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

74 plantings facilitate the long-term persistence of birds in fragmented landscapes?'

75

76 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;

78 Zanette 2001; Herkert *et al.* 2003; Debus 2006a; Debus 2006b; Holoubek and Jensen 2016), with a

results of comparative studies in fragmented and intact landscapes (e.g. Burke and Nol 2000;

80 Cooper et al. 2002; Luck 2003). The majority of earlier work in revegetated landscapes has focused

81 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.*

83 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.

86 The pressure of potential extinction debts for woodland birds (Ford et al. 2009) – that is, continued

87 declines even after habitat loss and degradation (or other challenges) are eliminated or reversed

88 (Kuussaari et al. 2009) – adds impetus to the need for replacing lost woodland habitat. However, it

89 is imperative the effects of revegetation on avifauna are more comprehensively understood, lest

90 they fail to address (or at worst, exacerbate) population declines.

91

92 Approach

93 In this paper, we review the current knowledge on avifaunal response to revegetation and habitat 94 restoration, and provide a general overview and synthesis of existing and future research directions 95 on the topic of woodland birds in restoration plantings. We focus largely on Australian temperate 96 woodlands, the cover of which has been reduced by up to 90% over the past 150 years as a result of 97 land clearing for agriculture (Paton and O'Connor 2010). We build on the preliminary overview by 98 Munro et al. (2007), consolidating the most recent research on the relationship between birds and 99 restoration plantings and examining the available information that underpins practical restoration of 100 woodland habitat. We move beyond the scope of previous reviews by exploring how the 101 implementation of restoration plantings might influence the long-term survival and persistence of

102 woodland bird communities in fragmented agricultural landscapes. Finally, we identify gaps in the

103 current knowledge and propose further research that would enhance understanding of the population

104 dynamics of woodland birds in restoration plantings and revegetated landscapes.

105

106 We identified relevant literature for this paper by searching publication databases and citation lists,

107 including ScienceDirect, Scopus and Google Scholar. We took a non-systematic approach and used

108 a broad range and combination of search terms, including 'woodland birds', 'breeding success',

109 'population dynamics', 'occupancy', 'distribution', 'revegetation' and 'restoration'. We searched

110 the internet and an institutional library catalogue for non-peer-reviewed work including books,

111 theses and reports.

112 Background

113 Habitat degradation and restoration

114 Temperate woodlands once covered an extensive area of southern Australia, however, the vast

115 majority has been cleared for agriculture since European settlement (Saunders and Curry 1990;

116 Lindenmayer et al. 2010a; Bradshaw 2012). Estimates vary, but around 32 million hectares, or up to

117 90%, of native temperate woodland vegetation cover has been cleared (Vesk and Mac Nally 2006;

118 Paton and O'Connor 2010). Scattered remnants persist, but due to their isolation and degradation

119 history, they are vulnerable to threatening processes such as agricultural intensification, grazing,

120 nutrient enrichment, weed invasion, and climate change (Eldridge 2003; Maron and Fitzsimons

121 2007; Duncan and Dorrough 2009; Mac Nally *et al.* 2009; Prober *et al.* 2012; 2014).

122

123 The negative effects of broad-scale habitat clearance on the Australian environment began to be

124 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

126 1980s and 1990s led to small-scale revegetation programs that were initially instigated by the

127 farming and environmental sectors to address issues such as salinity and erosion (Stirzaker *et al.*

128 2002; Campbell et al. 2017), with larger-scale government-initiated revegetation programs such as

129 the National Tree Program and the One Billion Trees Program applied within the next two decades

130 (Hajkowicz 2009; Lindenmayer *et al.* 2013). Many early plantings were implemented without a

131 well-defined wildlife conservation plan, but have nonetheless in some cases been occupied by

132 woodland birds and other fauna (Munro *et al.* 2007; Lindenmayer *et al.* 2016).

133

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;

136 Lindenmayer et al. 2013). Knowledge of effective revegetation techniques has also been used to 137 begin construction of large-scale habitat linkage corridors (e.g. Gondwana Link) through the 138 acquisition and revegetation of farming properties (Paton and O'Connor 2010). An ongoing (to 139 2020), large-scale government initiative is the 20 Million Trees Program, which aims to "improve 140 the extent, connectivity and condition of native vegetation", with explicit reference to threatened 141 species such as the southern emu-wren (Stipiturus malachurus) and regent parrot (Polytelis 142 anthopeplus) (Australian Government Department of the Environment and Energy 2017; Landcare 143 Australia 2017). Vegetation is also increasingly being planted for carbon sequestration, and such 144 plantings have the potential to enhance the conservation of biodiversity (Bradshaw et al. 2013;

- 145 Collard *et al.* 2013).
- 146

147 With ongoing large-scale revegetation programs such as the 20 Million Trees Program underway in 148 Australia, extensive areas of temperate woodland restoration plantings are being added to the 149 landscape every year (Atyeo and Thackway 2009; Campbell et al. 2017). However, it is important 150 to note that Australia's rate of land clearing remains among the highest in the world (Bradshaw 151 2012; Evans 2016). With an ongoing net loss of habitat, restoration plantings are a critical 152 conservation strategy for woodland birds and other fauna. Many restoration projects claim to focus 153 on creating habitat for threatened and/or declining wildlife (e.g. Landcare Australia 2017). There is 154 evidence that a focal-species approach can be used to develop guidelines for revegetation programs 155 (Freudenberger 2001; Freudenberger and Brooker 2004; Wood et al. 2004). However, its usefulness 156 as a conservation tool is debated (Lambeck 2002; Lindenmayer et al. 2002). Recent research 157 suggests that although the focal-species approach has some merit, it is also necessary to ensure the 158 flexibility of management actions such that all species are accounted for in conservation; focusing 159 on one species may not benefit others of conservation concern, especially those which might not 160 occur in species-rich assemblages (Lindenmayer et al. 2014). Furthermore, a generalised lack of 161 information on the habitat requirements and population processes of many threatened and declining 162 woodland bird species (Rayner et al. 2014) means that many revegetation programs are being 163 implemented without sufficient knowledge as to the habitat requirements of the species they should 164 be supporting (Block et al. 2001; Montague-Drake et al. 2009; Polyakov et al. 2015). 165 166 Reviews of restoration practice as early as the 1990s have outlined steps that should be taken to 167 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;
- 169 Lindenmayer et al. 2008; Duncan and Dorrough 2009; Prober and Smith 2009; Campbell et al.
- 170 2017); also see the National Standards for the Practice of Ecological Restoration in Australia

171 (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;
- 173 Ruiz-Jaen and Aide 2005; Herrick *et al.* 2006; Hobbs 2017). This should include assessing the
- 174 capacity of restoration plantings to support reproducing populations, an attribute that is rarely
- 175 measured in restoration monitoring projects (Ruiz-Jaen and Aide 2005; Vesk and Mac Nally 2006).

176 Patterns: bird responses to revegetation in Australian temperate woodlands

- 177 Many pattern-based studies have investigated the effects of habitat loss, fragmentation and
- 178 degradation on declining woodland bird species in Australia (reviewed by Ford et al. 2001; Ford
- 179 2011); fewer have examined how these species respond to restoration plantings (Nichols and
- 180 Watkins 1984; Heath 2003; Robinson 2006; Lindenmayer et al. 2007; Barrett et al. 2008;
- 181 Cunningham et al. 2008; Saunders and Nicholls 2008; Loyn et al. 2009; Selwood et al. 2009;
- 182 Lindenmayer et al. 2010b; Munro et al. 2011; Shanahan et al. 2011; Lindenmayer et al. 2012;

183 Bennett et al. 2013; Vesk et al. 2015). To date, much of the research on birds in revegetated

184 landscapes has focused on answering the question 'Do birds use restoration plantings?', and

- 185 concurrently, 'Which plantings are preferentially selected?'
- 186

187 Previous research has discovered that some woodland bird species, including species of 188 conservation concern, will readily occupy restoration plantings, and may even preferentially select 189 plantings over remnant woodland (Nichols and Watkins 1984; Heath 2003; Kinross 2004; Martin et 190 al. 2004; Kavanagh et al. 2007; Cunningham et al. 2008; Saunders and Nicholls 2008; Loyn et al. 191 2009; Lindenmayer et al. 2010b; Martin et al. 2011; Lindenmayer et al. 2012). These species have 192 been termed 'planting specialists' – species that are more likely to be found in restoration plantings 193 than in woodland remnants (Table 1). It should be noted that inferred habitat preferences for some 194 species, such as the eastern yellow robin, scarlet robin, and southern whiteface (see Table 1 for 195 scientific names), are not consistent among studies.

196

197 TABLE 1

198

199 Bird species occupancy and abundance in restoration plantings appears to be a complex relationship

- 200 between context (location within the landscape, e.g. proximity to other areas of native vegetation),
- 201 configuration (e.g. shape, area), and content (structural and floristic variables) (Nichols and Watkins
- 202 1984; Kavanagh et al. 2007; Cunningham et al. 2008; Kinross and Nicol 2008; Lindenmayer et al.
- 203 2010b; Munro et al. 2011; Lindenmayer et al. 2016) (Table 2). Differences in bird community
- 204 composition in restoration plantings and remnant woodland have been consistently reported in

205 Australia (Arnold 2003; Loyn et al. 2007; Martin et al. 2011; Munro et al. 2011; Lindenmayer et al. 206 2012), as well as in similarly restored habitat patches in Brazil (Becker et al. 2013), China (Zhang 207 et al. 2011), Mexico (MacGregor-Fors et al. 2010), and the United States (Brawn 2006; Ortega-208 Alvarez *et al.* 2013). Some studies note that the bird community continually changes following 209 initial establishment as planted vegetation matures and becomes more similar to remnant habitat 210 (Lindenmayer et al. 2016; Debus et al. 2017); generalists and species favoured by open habitats are 211 more common in the early stages, while shrub-dwelling and canopy specialists colonise as the 212 habitat structure develops over time (Twedt et al. 2002; Heath 2003; Jansen 2005; Freeman et al. 213 2009; Gould and Mackey 2015).

214

215 Habitat composition and structure strongly influence bird community composition and abundance 216 in restoration plantings (Arnold 2003; Barrett et al. 2008; Munro et al. 2011; Gould and Mackey 217 2015). In general, woodland bird abundance and diversity appears to increase with habitat 218 complexity – the inclusion of a more diverse plant species assemblage, leaf litter, and an increase in 219 canopy cover have all been positively associated with bird species richness and abundance (Barrett 220 et al. 2008; Bonifacio et al. 2011; Munro et al. 2011; Gould and Mackey 2015). It is important to 221 recognise the diverse ways in which different species or foraging guilds may respond to habitat 222 features in restoration plantings. For example, Comer and Wooller (2002) found that a "clumped" 223 spatial arrangement of shrubs in restoration plantings facilitated competitive exclusion of small 224 honeyeaters by larger species, decreasing overall nectarivore diversity in the plantings. Barrett et al. 225 (2008) found that ground-foraging insectivores were underrepresented in restoration plantings, and 226 postulated that lack of native forb diversity may have been a likely cause. According to Arnold 227 (2003), the inclusion of canopy and perching sites within one metre of the ground results in a 228 greater abundance of insectivores in restoration plantings. Martin et al. (2004) found significantly 229 lower abundances of species who primarily forage on bark in restoration plantings compared to 230 woodland remnants; this may be due in part to the fact that certain habitat features, such as 231 decorticating bark and fallen timber, take decades or even centuries to develop in temperate 232 woodland habitats (Cunningham et al. 2007; Mac Nally 2008; Vesk et al. 2008; Munro et al. 2009). 233 This may also be why restoration plantings are not predicted to support certain woodland-dependent 234 bird species until 40, 60, or 100 years after establishment (Thomson et al. 2009). 235 236 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
- 239 rufous whistler (*Pachycephala rufiventris*) and grey fantail (*Rhipidura albiscapa*) are two species

7

- 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
- 242 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*).
- 245

246 TABLE 2

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

248 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

250 must be able to gain required resources from the patch they select (or from adjacent areas). This

- 251 includes resources such as food and nesting sites, but also habitat services such as adequate
- 252 protection from predation and competition (Figure 1).
- 253

254 FIGURE 1

255

256 There is documented evidence of breeding activity and site fidelity in multiple woodland bird 257 species colonising young restoration plantings (2-3 years old) (Barrett et al. 2008). Bird breeding 258 activity also has been reported in more mature plantings (up to 26 years old for directly planted 259 sites, and 111 years for restored woodland remnants) (Selwood et al. 2009; Mac Nally et al. 2010; 260 Bond 2011). However, species preference for, and occupancy of, a given habitat type is not 261 necessarily correlated with long-term survival and persistence (Van Horne 1983; Battin 2004; Loyn 262 et al. 2009). This is particularly relevant for declining species, which may occupy a site but display 263 only limited evidence of successful breeding (Selwood et al. 2009; Mac Nally et al. 2010). 264

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).

271 Individuals may also inadvertently avoid high-quality patches due to misleading habitat cues, which

- 272 likewise creates an ecological trap mechanism at the landscape level (Gilroy and Sutherland 2007).
- 273 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 extensiveplanting of native vegetation (Figure 2).

276

277 FIGURE 2

278

279 There are some instances in the global literature of restored habitats acting as ecological traps. For 280 example, Larison et al. (2001) found that the song sparrow (Melospiza melodia) in restored riparian 281 forest in California had lower reproductive success than in naturally regenerating or mature forest, 282 due to the restored stands providing fewer nesting site choices and less protection from predation. 283 Managed prairie sites were described as ecological traps by Shochat *et al.* (2005), as higher 284 invertebrate abundances attracted breeding birds which subsequently experienced poorer nesting 285 success than in other sites. Chalfoun and Martin (2007) also documented lower nest success of 286 Brewer's sparrow (Spizella breweri) in North American shrub-steppe landscapes with greater shrub 287 cover, despite greater densities of birds settling in these landscapes. Low-density populations, such 288 as those of many declining woodland bird species in Australia, face a high risk of local extinction in 289 ecological traps (Kokko and Sutherland 2001). Many Australian woodland birds are relatively long-290 lived – 10-20 years is common in many species (Australian Bird and Bat Banding Scheme 2016). 291 Consequently, there may be a time-lag before the effects of a potential ecological trap mechanism 292 become apparent. It is therefore important to assess whether woodland birds are able to successfully 293 breed in restoration plantings. In the following sections, we discuss the primary factors likely to 294 influence the reproductive success of breeding birds in restoration plantings.

295

296 *Nest predation*

297 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

301 studies to date have sought to quantify nest predation or nest success in Australian temperate

302 woodland restoration plantings. Typical predation rates on the nests of birds vary greatly between

- 303 species, even for those with similar nest structures (Ford *et al.* 2001; Weidinger 2002). For
- 304 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
- 306 cause of failure (Robinson 1990; Zanette and Jenkins 2000; Armstrong et al. 2002; Debus 2006c).
- 307 Conversely, fantails (Rhipiduridae) typically have a 59-71% nest success rate, despite building cup-

308 nests that are less cryptic than those of robins (Cameron 1985). Parental behaviour, brood behaviour

309 (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

311 communities (Martin *et al.* 2000; Haskell 2002; Weidinger 2002; Haff and Magrath 2011;

312 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

314 importance of conducting such studies in restoration plantings.

315

316 Nest predation is also fundamentally dependent on the type and abundance of predators in the

317 vicinity of the nest (Muchai and du Plessis 2005; Guppy *et al.* 2017). Avian predators cause up to

318 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

320 magpie (*Cracticus tibicen*), have been favoured by habitat loss and fragmentation in temperate

321 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

323 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

325 considerable effort and resources required, in addition to the complex ecological and ethical

326 considerations associated with controlling native predators (Wallach *et al.* 2010; 2015).

327

328 Patch size and isolation can interact with predation risk to influence breeding success and thus 329 recruitment and persistence of birds in fragmented landscapes (reviewed by Stephens et al. 2004). 330 Studies in fragmented landscapes worldwide have recorded lower breeding success and 331 reproductive output in smaller habitat patches than in larger patches (Hoover *et al.* 1995; Burke and 332 Nol 2000; Zanette and Jenkins 2000; Zanette 2001; Walk et al. 2010). These findings are frequently 333 attributed to 'edge-effects', i.e. increased nest predation near habitat edges (Hoover *et al.* 1995; 334 Burke and Nol 2000; Willson et al. 2001; Vander Haegen et al. 2002; Herkert et al. 2003; Wozna et 335 al. 2017). However, this notion is challenged by other studies reporting no difference in nesting 336 success or recruitment in smaller fragments (Lehnen and Rodewald 2009; Lollback et al. 2010; 337 Walk et al. 2010) and/or no evidence of edge-effects increasing predator activity on nests (Hanski et 338 al. 1996; Lahti 2001; Woodward et al. 2001; Piper et al. 2002; Boulton and Clarke 2003; Reino et 339 al. 2010). It is important to consider the spatial scale of fragmentation relative to nest predation and 340 its potential effects on bird populations – that is, whether fragmentation is occurring at the 341 landscape, patch or edge scale (Zanette and Jenkins 2000; Stephens et al. 2004). Furthermore,

342 different predation processes, including different primary predators, may operate in fragmented

343 versus intact landscapes (Vander Haegen *et al.* 2002).

344

345 The contrasting outcomes of studies of nest success in fragmented landscapes imply that the effects 346 of influential processes are either species-specific or landscape-dependent or both. In general, we 347 might expect species that typically experience high levels of nest predation to experience greater 348 nest success in larger restoration plantings, or in plantings surrounded by a greater amount of 349 vegetation cover. However, surrounding land-use may have unexpected effects on the distribution 350 and abundance of nest predators and thus nesting success, irrespective of patch size or connectivity. 351 Indeed, a recent study by Okada et al. (2017) found effects of both nest type and the surrounding 352 matrix (i.e. land use) on breeding success of small-bodied woodland birds in a fragmented 353 landscape. The results were contrary to expectations – nesting success for dome-nesting species was 354 higher in woodland patches surrounded by grazing land than patches surrounded by pine 355 plantations, with abundance of avian predator nests thought to be a contributing factor. Monitoring 356 nest predation and success is an under-utilised pathway to understanding which species are being 357 supported in the long term, and enabling management decisions to tailor restoration programs for 358 species more vulnerable to predation. These topics should be thoroughly investigated in future 359 research.

360

361 Nest site selection

362 The importance of nest site microhabitat selection in bird breeding success has been documented 363 both internationally (Martin 1998; Mezquida 2004; Smith et al. 2009; Schlossberg and King 2010; 364 Murray and Best 2014) and in Australia (Oliver et al. 1998; Cousin 2009; Soanes et al. 2015). 365 However, research concerning woodland species nesting in restoration plantings is lacking, and may 366 be a critical determinant of breeding success (Martin 1998). This is particularly relevant for species 367 vulnerable to predation, such as cup-nesters (Okada et al. 2017). Nest-site selection for such species 368 may act as a stronger selective pressure than other variables. For example, the western yellow robin 369 (Eopsaltria griseogularis) favours sites with views of the nest surroundings over foraging 370 opportunities when selecting a nest site (Cousin 2009), indicating that predation is a primary 371 concern for nesting individuals of this species. It is crucial that restoration plantings provide 372 suitable nesting sites for a range of woodland bird species, lest they fail to support breeding 373 populations (Larison et al. 2001). For example, the inclusion of trees with dense and/or pendulous 374 foliage may increase availability of well-concealed nesting sites for foliage-nesters such as the 375 weebill and yellow thornbill. Species that nest in lower strata, such as the superb fairy-wren and 376 speckled warbler, may be better supported with the presence of native grasses and/or the

377 accumulation of dead woody material and leaf litter in the ground layer. These are factors rarely

378 considered when constructing or monitoring restoration plantings.

379

380 *Resource availability*

381 Resource distribution and abundance in habitat patches are critical determinants of woodland bird 382 site occupancy and foraging patterns (Gilmore 1986; Barrett et al. 2008; Vesk et al. 2008; 383 Montague-Drake et al. 2009; Munro et al. 2011). For example, litter and bare ground are important 384 habitat features supporting ground-foraging birds such as robins and thornbills (Bromham et al. 385 1999; Antos and Bennett 2006). Species in these groups also prefer a low density of shrubs, as does 386 the diamond firetail (Antos et al. 2008). Other species may rely on various other resources, such as 387 woody debris – reintroduced brown treecreepers in a vegetation reserve responded positively only 388 when woody debris was included as a habitat feature (Bennett et al. 2013). A lack of woody debris 389 may be one reason the brown treecreeper is currently underrepresented in restoration plantings 390 (Martin et al. 2004; 2011; Lindenmayer et al. 2012; Gould and Mackey 2015). Furthermore, 391 woodland bird species, including the brown treecreeper and southern whiteface, are known to vary 392 their foraging habits and use of foraging substrates between the breeding and non-breeding seasons 393 (Antos and Bennett 2006). This highlights the importance of using prior knowledge of species' 394 habitat requirements to inform predicted responses of birds to habitat restoration (Bennett et al.

395

2013).

396

397 Food is generally considered a limiting resource for breeding birds (von Brömssen and Jansson 398 1980; Hochachka and Boag 1987; Simons and Martin 1990; Verhulst 1994; Granbom and Smith 399 2006; Wellicome et al. 2013). However, the addition of food resources does not tend to prevent 400 major declines in fluctuating populations of terrestrial vertebrates (Boutin 1990), suggesting that the 401 mechanisms of species decline are not usually related to resource-limitation alone. Nonetheless, it is 402 vital to assess the role of food resources in woodland bird habitat suitability. The study by Zanette 403 et al. (2000) is unique in its exploration of food shortage affecting birds in fragmented Australian 404 woodlands; the authors documented lower availability of food resources in smaller versus larger 405 fragments, with breeding success found to be lower in smaller fragments. Restoration plantings 406 overwhelmingly comprise small habitat patches (Freudenberger et al. 2004; Smith 2008), and are 407 known to attract a variety of bird species, including species of conservation concern (Lindenmayer 408 et al. 2010b). When colonising sites, birds are motivated by habitat cues indicative of high resource 409 availability, such as vegetation structure (Kokko and Sutherland 2001). If resource availability in 410 restoration plantings does not accurately reflect these cues, then there is an increased likelihood of 411 ecological trap mechanisms operating in revegetated landscapes (Schlaepfer et al. 2002).

412

413 Home range sizes of birds are inversely related to resource density and resource renewal rates (Ford 414 1983). This means that larger home ranges are required in habitats with fewer available resources. 415 In a fragmented landscape, birds that are unwilling to cross habitat gaps may be disadvantaged if 416 they are unable to expand their home ranges to exploit resources in adjacent patches (Fahrig 2007; 417 Robertson and Radford 2009). Patchily distributed or scarce food resources can lead to inefficient 418 foraging patterns, with subsequent reduced fitness and reproductive output in birds (Pyke 1984; 419 Martin 1987; Granbom and Smith 2006; Flockhart et al. 2016). In the breeding season, optimal 420 central place foraging (i.e. the need to regularly return to the nest) influences searching movements, 421 distance travelled, and prey selection (Pyke 1984). In a fragmented landscape, the need to expand 422 foraging areas or depart a patch due to resource depletion can measurably increase energy 423 expenditure for breeding birds, thus reducing their reproductive fitness. For example, birds in 424 fragmented landscapes may spend up to 64% more energy per chick raised than those breeding in 425 intact remnant woodland (Hinsley et al. 2008). Small woodland patches have also been associated 426 with the contraction of breeding seasons, eggs of lighter mass being laid, and smaller nestlings 427 being produced (Zanette et al. 2000). These issues could influence the breeding success of birds in 428 restoration plantings.

429

430 For insectivorous birds in particular, dietary composition and hence dietary quality is directly 431 related to habitat quality (Razeng and Watson 2012). Terrestrial invertebrates can display strong 432 responses to habitat variables in fragmented temperate woodlands (Bromham et al. 1999; Barton et 433 al. 2009; Lindsay and Cunningham 2009; Gibb and Cunningham 2010). As an example, Zanette et 434 al. (2000) identified a 50% lower biomass of surface-dwelling invertebrates in small (55 ha) relative 435 to large (>400 ha) woodland fragments, thereby linking food resources for insectivorous birds to 436 patch size. Coleoptera constitute the largest proportion of prey items for declining insectivorous 437 woodland birds, followed by Formicidae and Lepidoptera (Razeng and Watson 2012). Coleoptera 438 and other preferred prey of insectivorous birds have been shown to respond positively to some 439 restoration treatments (e.g. removal of grazing pressure, addition of fallen logs to habitat patches) 440 (Lindsay and Cunningham 2009; Gibb and Cunningham 2010). However, there is also evidence that 441 restoration plantings may not help restore invertebrate communities in agricultural landscapes 442 (Jellinek et al. 2013). It is important to understand and consider the effects of habitat fragmentation 443 and restoration on invertebrate prev of woodland birds when assessing habitat quality in restoration 444 plantings.

445

13

446 *Competition*

447 Interspecific competition for resources is a strong selective process that is enhanced in habitats with 448 depleted or patchy resources (Cody 1981). Sought-after resources such as food and nesting sites are 449 defended by birds in established territories, especially during the breeding season (Robinson 1989; 450 Broughton et al. 2012; Belder 2013). Closely-related species may compete for similar resources, 451 particularly food. For example, Robinson (1990) found that flame robins and scarlet robins compete 452 more for food resources than nest sites. The noisy miner (Manorina melanocephala) is a strong 453 competitor for territories and resources in Australian temperate woodlands, and actively disrupts 454 and excludes other small woodland birds (Grey et al. 1998; Maron 2007; Montague-Drake et al. 455 2011; Maron et al. 2013; Bennett et al. 2015). Competition from the noisy miner has been shown to 456 decrease breeding activity in species of smaller body mass, and can have a greater influence on 457 woodland bird distribution and recruitment than vegetation characteristics (Bennett *et al.* 2015; 458 Mortelliti *et al.* 2016). Recent research has revealed that the noisy miner is both increasing the risk 459 of woodland birds going extinct from habitat patches, and decreasing the chances of them 460 colonising patches (Mortelliti et al. 2016). The composition of restoration plantings can 461 significantly affect the likelihood of colonisation and occupancy by the noisy miner; inclusion of a 462 *Eucalyptus* overstorey increases the likelihood of noisy miner colonisation as the vegetation 463 matures (Maron 2007). Conversely, the inclusion of an Acacia understorey reduces noisy miner 464 occupancy (Lindenmayer et al. 2010b). Monitoring restoration plantings for factors likely to 465 increase competition and competitive exclusion will provide a better understanding of species 466 persistence mechanisms in these environments.

467

468 Brood parasitism

469 The influence of brood parasitism on nest success is a factor often discussed in international studies

470 of habitat restoration (Delphey and Dinsmore 1993; Fletcher *et al.* 2006; Small *et al.* 2007;

471 Forrester 2015), but limited research has been done on this topic in Australian temperate woodland

472 ecosystems (Ford 2011) – but see Guppy *et al.* (2017). There is evidence suggesting that parasitic

473 cuckoos are dependent on large woodland remnants with an abundance of their preferred host

- 474 species, and that host species may experience greater breeding success in smaller fragments where
- 475 cuckoos are rare (Brooker and Brooker 2003). Restoration plantings typically create small habitat
- 476 patches (Freudenberger *et al.* 2004; Smith 2008), thus brood parasitism events may be infrequent in
- 477 revegetated sites. However, to our knowledge, no empirical studies to date have documented brood
- 478 parasitism in temperate woodland restoration plantings, so its potential effect on the reproductive
- 479 success of woodland birds in revegetated landscapes remains unknown.

480 Summary and future research directions

481 Research to date has shown that the responses of woodland birds to revegetation are varied, and 482 while the habitat requirements of some species may be met, there is still much to learn about the 483 long-term responses of birds to landscape-scale habitat restoration. Ostensibly, occupancy data 484 alone may not expose underlying trends in population processes, or drivers of breeding success and 485 site fidelity. To prevent and reverse the ongoing decline of Australia's woodland avifauna, and re-486 establish endangered habitat in highly fragmented agricultural landscapes, it is vital that temperate 487 woodland restoration efforts continue and increase over the coming years. However, to ensure that 488 restoration plantings are both an ecologically-effective and cost-effective biodiversity conservation 489 strategy, it is also essential for their design and management to be informed by scientific research. 490

491 There is an increasing number of modelling studies proposing strategies for optimising landscape

492 restoration, aiming to solve the issues of catering for multiple species and ensuring maximum cost-

493 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

496 *et al.* 2016). Many of these studies provide information to help guide future restoration efforts in

497 Australia. However, because conservation and restoration remain low priorities for governments,

498 almost all the proposed strategies are yet to be empirically tested. Furthermore, to the best of our

499 knowledge, all such studies are based on pattern data. Due to the lack of knowledge on population

500 processes in revegetated landscapes, optimisation strategies for restoration to support breeding

501 populations of woodland birds are non-existent.

502

503 Developing a comprehensive understanding of woodland bird ecology in revegetated landscapes is 504 fundamental to devising knowledge-based solutions to reverse species decline (Bennett and Watson 505 2011), and a necessary key step is to move beyond pattern data towards quantifying population 506 responses of birds to habitat restoration. We suggest that future research in restoration plantings 507 should focus on the areas of interest and knowledge gaps identified by this review (summarised in 508 Table 3), with an emphasis on exploring factors at the landscape- and patch-scale that are likely to 509 contribute to restoration plantings acting as ecological traps. In particular, based on our review, we 510 suggest the following questions should be addressed as priorities:

- 511 What cues do birds use to select habitat in revegetated landscapes?
- 512 Are woodland birds resident in restoration plantings in the long term?
- 513 Do restoration plantings have higher immigration and/or mortality rates than woodland
 514 remnants?

515	- Is habitat quality in restoration plantings sufficient for woodland birds to breed successfully?
516	- Does habitat suitability for breeding birds change over time as plantings mature?
517	- How does the breeding success of birds in plantings compare to that of birds in remnant
518	woodland?
519	- What are the primary nest predators and rates of nest failure due to predation?
520	- Do restoration plantings provide suitable nesting sites and adequate food resources for
521	woodland birds?
522	- What is the role of competitive exclusion by the noisy miner?
523	- What is the role of brood parasitism in restoration plantings?
524	
525	Finally, a more thorough approach to monitoring restored habitats is required to determine their
526	ability to support breeding populations of woodland birds. As Battin (2004) emphasised, 'we
527	cannot afford to ignore the possibility of ecological traps or fail to take them into account in the
528	study, management, and conservation of animal populations.' Crucially, the capacity to accurately
529	evaluate the success of restoration plantings in achieving intended conservation goals underpins
530	effective utilisation of conservation resources, as well as ecologically sound environmental
531	management.
532	
533	TABLE 3

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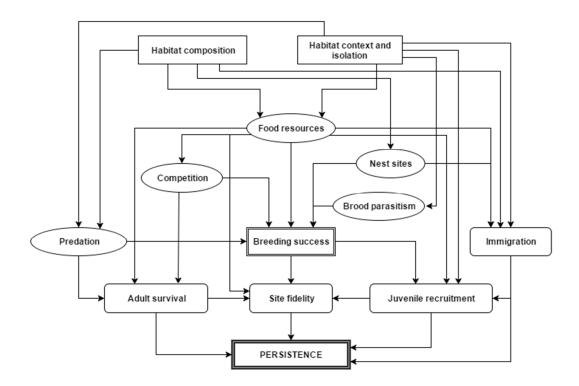


Figure 1 Conceptual diagram of interrelated factors that may influence the breeding success and persistence of woodland bird populations in restoration plantings. Bold/double rectangles = the processes we focus on in this review (breeding success and persistence). Rounded rectangles = population processes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

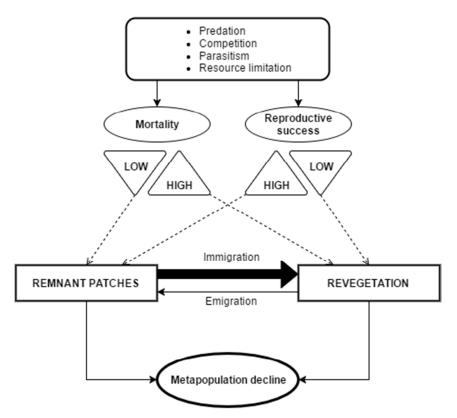


Figure 2 A conceptual model of an ecological trap mechanism operating in a fragmented landscape with restoration plantings and remnant patches. Restoration plantings have the potential to become ecological traps if they are preferentially occupied but lead to lower reproductive success and/or higher mortality than remnant patches. O = population process, \triangle = trend in population process, \square = 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).

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·		Petroica goodenovii	Cunningham <i>et al.</i> 2008; Lindenmayer <i>et al.</i> 2012	South-west Slopes, NSW
flame robin ^{CV} <i>Petroica phoenicea</i> Lindenmayer <i>et al.</i> 2012 South-west Slopes, NSW		Petroica phoenicea	Lindenmayer <i>et al.</i> 2012	South-west Slopes, NSW
hooded robin ^{CV} Melanodryas cucullata Cunningham et al. 2008 South-west Slopes, NSW	hooded robin ^{CV}	Melanodryas cucullata	Cunningham <i>et al.</i> 2008	South-west Slopes, NSW
eastern yellow robin <i>Eopsaltria australis</i> Cunningham <i>et al.</i> 2008 South-west Slopes, NSW	•	•	-	•
red-browed finch Neochmia temporalis Kavanagh et al. 2007; South-west Slopes, NSW Barrett et al. 2008; Cunningham et al. 2008; Lindenmayer et al. 2012	red-browed finch	Neochmia temporalis	Barrett <i>et al.</i> 2008; Cunningham <i>et al.</i> 2008;	South-west Slopes, NSW
diamond firetail ^{CV} Stagonopleura guttata Cunningham et al. 2008 South-west Slopes, NSW	diamond firetail ^{CV}	Stagonopleura guttata	Cunningham <i>et al.</i> 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 <i>et al.</i> 2008; Selwood <i>et al.</i> 2009; Lindenmayer <i>et al.</i> 2010b; Munro <i>et al.</i> 2011	Goomalling Shire, WA; Box-ironbark region, VIC; South-west Slopes, NSW West Gippsland, VIC
Configuration	Shape	Lindenmayer <i>et al.</i> 2010b	South-west Slopes, NSW
	Area	Selwood <i>et al.</i> 2009; Lindenmayer <i>et al.</i> 2010b; Munro <i>et al.</i> 2011	Box-ironbark region, VIC South-west Slopes, NSW West Gippsland, VIC
	Topography	Lindenmayer <i>et al.</i> 2010b	South-west Slopes, NSW
Content	No. plants	Lindenmayer <i>et al.</i> 2010b	South-west Slopes, NSW
	No. native plant species	Barrett <i>et al.</i> 2008; Munro <i>et al.</i> 2011	South-west Slopes, NSW West Gippsland, VIC
	Canopy depth	Lindenmayer <i>et al.</i> 2010b	South-west Slopes, NSW
	Canopy height	Lindenmayer <i>et al.</i> 2010b	South-west Slopes, NSW
	Overstorey cover	Barrett <i>et al.</i> 2008; Lindenmayer <i>et al.</i> 2010b	South-west Slopes, NSW
	Midstorey cover	Barrett <i>et al.</i> 2008; Lindenmayer <i>et al.</i> 2010b	South-west Slopes, NSW
	Understorey/ground cover	Heath 2003; Arnold 2003; Barrett <i>et al.</i> 2008; Lindenmayer <i>et al.</i> 2010b	Goomalling Shire, WA; Wandoo woodland, WA; South-west Slopes, NSW
	Mistletoe	Lindenmayer <i>et al.</i> 2010b	South-west Slopes, NSW
	Logs, fallen timber, leaf litter	Barrett <i>et al.</i> 2008; Selwood <i>et al.</i> 2009; Lindenmayer <i>et al.</i> 2010b; Munro <i>et al.</i> 2011	Box-ironbark region, VIC South-west Slopes, NSW West Gippsland, VIC
	Dead trees/shrubs	Lindenmayer <i>et al.</i> 2010b	South-west Slopes, NSW
	Remnant/paddock trees	Selwood <i>et al.</i> 2009; Lindenmayer <i>et al.</i> 2010b; Munro <i>et al.</i> 2011	Box-ironbark region, VIC South-west Slopes, NSW West Gippsland, VIC
	Grazing	Selwood <i>et al.</i> 2009; Lindenmayer <i>et al.</i> 2010b	Box-ironbark region, VIC South-west Slopes, NSW
Other	Age	Selwood <i>et al.</i> 2009; Munro <i>et al.</i> 2011	Box-ironbark region, VIC West Gippsland, VIC
	Vegetation condition	Munro <i>et al.</i> 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 <i>et al.</i> 2011; Lindenmayer <i>et al.</i> 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 <i>et al.</i> 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 <i>et al.</i> 2000)	Food resource availability lower in smaller than in larger woodland fragments	Resources in restored landscapes (e.g. Le Roux <i>et al.</i> 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 <i>et al.</i> 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 <i>et al.</i> 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 <i>et al.</i> 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 <i>et</i> <i>al.</i> 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 <i>et al.</i> 2001)	Brood parasitism by brown-headed cowbirds (<i>Molothrus ater</i>) lower in restored than in remnant landscapes	Brood parasitism in Australian temperate woodlands	Horsfield's bronze- cuckoo (<i>Chalcites</i> <i>basalis</i>) 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 <i>et al.</i> 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 <i>et al.</i> 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