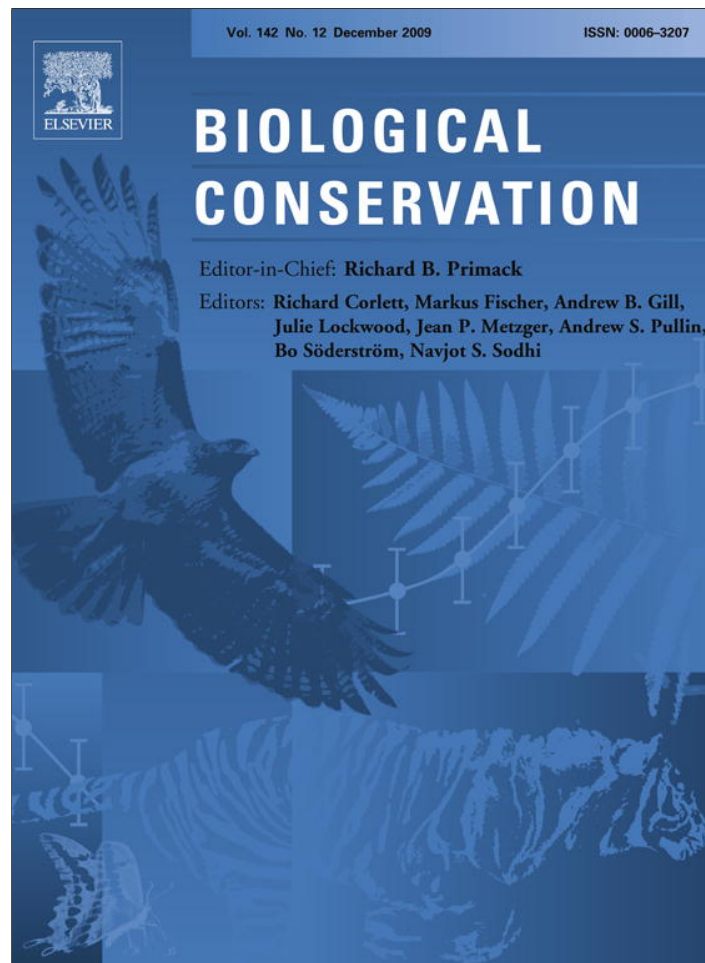


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## Extinction debt or habitat change? – Ongoing losses of woodland birds in north-eastern New South Wales, Australia

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### ABSTRACT

The loss, fragmentation and degradation of native vegetation are major causes of loss of biodiversity globally. Extinction debt is the term used to describe the ongoing loss of species from fragmented landscapes long after the original loss and fragmentation of habitat. However, losses may also result from habitat changes that are unrelated to fragmentation, which reduce breeding success and recruitment. Many woodland birds have declined in fragmented landscapes in Australia, probably due to loss of small, isolated populations, though the ecological processes are poorly understood. We record the progressive regional loss of two ground-foraging, woodland birds, the Brown Treecreeper *Climacteris picumnus* and Hooded Robin *Melanodryas cucullata*, in northern New South Wales, over 30 years. This has happened despite most habitat loss occurring over 100 years ago, suggesting the payment of an extinction debt. Our observations suggest that several ecological processes, caused by habitat loss, fragmentation or degradation, and operating over different time scales, have led to both species' declines. Female Brown Treecreepers disperse poorly among vegetation remnants, leaving only males in isolated populations, which then go extinct. In contrast, Hooded Robins suffer high nest predation in fragmented landscapes, producing too few recruits to replace adult mortality. Foraging by both species may also be affected by regrowth of ground vegetation and shrubs. We found little support for a major role played by drought, climate change or aggressive Noisy Miners *Manorina melanoccephala*. We propose that both extinction debt in the classical sense and ongoing habitat change frequently contribute to species' decline in modified landscapes. Management to arrest and reverse such declines needs to consider these multiple causes of decline. For instance, reconnecting isolated populations may be inadequate alone, and activities such as appropriate grazing, fires and the addition of woody debris may also be required.

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### 1. Introduction

Substantial areas of native vegetation in many parts of the world have been cleared for agriculture, so that in some regions less than 10% of original vegetation remains (Saunders et al., 1991). Such habitat loss usually leads directly to at least proportional declines of the populations of many birds and other organisms (Connor and McCoy, 1979; Woinarski et al., 2006). However, when the amount of native vegetation in a region drops below about 20–30%, fragmentation of the remaining vegetation may lead to disproportionate reductions in populations (Andr en, 1994; Fahrig, 1997; Radford et al., 2005). Individual remnants lose species due to chance extinctions, the negative effects of habitat edges, the inability or unwillingness of animals to disperse among iso-

lated remnants and loss of key resources. These local species losses may accumulate until a species goes extinct locally and even regionally (Saunders, 1989).

There is often a considerable lag between habitat loss and fragmentation and local extinctions, which has been called the extinction debt (Tilman et al., 1994). Malanson (2008) traces the development of the concept of extinction debt, which emerged from the Theory of Island Biogeography (MacArthur and Wilson, 1967). Because species richness on an island depended on a balance between colonisation (a function of isolation) and extinction rates (a function of island area), islands that become smaller or more isolated should lose species. Diamond (1975) illustrated this by showing how land bridge islands off New Guinea held more bird species than expected from their area and isolation, arguing that their fauna had not had time to relax since sea levels rose to isolate the islands from the mainland. The loss of some 45 bird species over about 60 years on Barro Colorado Island, a man-made island

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in the Panama Canal, indicates that species relaxation can be both substantial and rapid (Willis, 1974). Diamond (1975) also suggested that superior competitors tended to occupy species-rich islands and good dispersers species-poor islands. Hence, he implied that good competitors may be especially susceptible to species relaxation.

Many researchers applied the idea of species relaxation to the impact of habitat fragmentation. For instance, substantial species loss has occurred in forest remnants in both the Atlantic coast of Brazil (Christiansen and Pitter, 1997) and in Kenya (Brooks et al., 1999). Such loss is even more extreme in natural islands that become deforested, such as Singapore (Castelletta et al., 2000). Tilman et al. (1994) defined the term extinction debt as time-delayed but deterministic extinction, and developed models showing how dominant species are more likely to be lost from remnants and fragmented landscapes. Since that time, the term has been used frequently in relation to habitat fragmentation (e.g., Possingham and Field, 2001), though many models have focussed on the competition–colonisation dichotomy (Malanson, 2008). The ecological processes involved in ongoing loss of species are still poorly understood and are typically inferred from studies of species diversity in remnants relative to size and isolation (Metzger et al., 2009). The original concept of extinction debt focused on stochastic population fluctuations leading to local extinctions, which were not reversed by recolonisation due to the isolation of patches.

Habitat often becomes degraded as a result of fragmentation, which affects the survival and reproductive success of many species (Saunders et al., 1991). This too may lead to extinction some time after initial habitat loss and fragmentation. Loss through habitat degradation can be seen either as an expansion of the extinction debt concept, or as an alternative explanation for ongoing extinctions. Habitat quality may include factors such as the density of nest predators and competitors, as well as floristics and habitat structure (Ford et al., 2001). The latter two may affect the abundance and availability of food, and habitat structure may influence safe nesting sites and refuges from predators. Whereas habitat fragmentation may reduce habitat quality, changes in management may also affect habitat quality, even without fragmentation. For instance, changes in the intensity and frequency of fire and grazing may alter the structure of ground and understorey vegetation. With et al. (2008) studied three common birds in a large area of North American tall grass prairie. The birds showed chronically low breeding success, which With et al. attributed to the current pattern of grazing and burning. They estimated annual declines in their species of 3–29%. Hence, a lack of potential dispersers rather than inability to disperse was the problem.

Numerous species of birds that inhabit eucalypt woodlands in south-eastern Australia have declined in recent decades (Robinson and Trail, 1996; Reid, 1999; Barrett et al., 2003; Olsen et al., 2005). There is also evidence for species relaxation in fragmented landscapes long after the initial habitat loss. For instance, MacHunter et al. (2006) described the loss of bird species in open forest remnants in Victoria over 22 years. There have been many broad-scale studies of the patterns of distribution of eucalypt woodland bird species across fragmented and degraded landscapes. These have identified how patch size and isolation may influence the probability of occurrence of a species in a remnant (e.g. Howe, 1984; Seddon et al., 2003; Watson et al., 2005). However, fewer studies have focused on the actual ecological processes (e.g. reproduction, dispersal, etc.) and how they affect individual species (Ford et al., 2001). Walters et al. (1999) suggested ten alternative hypotheses to explain how habitat loss, fragmentation and degradation may lead to declines in bird species, but most of them remain largely untested. One of the best-supported hypotheses is that Noisy Miners (*Manorina melanocephala*) increase in fragmented and degraded habitat and aggressively exclude most other bird species (Maron,

2007). Grey et al. (1998) showed that when Noisy Miners are removed from woodland remnants the abundance and diversity of other birds increases rapidly.

Two groups, the treecreepers (Climacteridae) and robins (Petroicidae) have often been the focus of process-based research. Brown Treecreepers (*Climacteris picumnus*) in eastern Australia (Walters et al., 1999; Cooper et al., 2002; Cooper and Walters, 2002a, b), Rufous Treecreepers (*C. rufa*) in south-western Australia (Luck, 2002a, b, 2003) and White-browed Treecreepers (*C. affinis*) in inland eastern Australia (Radford and Bennett, 2004) all appear sensitive to habitat loss and fragmentation. Brown Treecreepers are often absent from isolated patches in northern New South Wales, or if present, the groups lack females (Walters et al., 1999; Cooper et al., 2002). Breeding success and foraging behaviour differ little between isolated and connected patches (Walters et al., 1999; Cooper and Walters, 2002a). Females translocated to isolated patches with males often stayed and even bred, indicating that absence from many isolated patches was the result of the inability of dispersing females to find them. (Cooper and Walters, 2002b).

The number of hollows, in which Brown Treecreepers nest, was the only habitat variable that was related to the species' presence, once isolated sites were removed from the analysis (Cooper and Walters, 2002a). However Doerr et al. (2006), in a large patch of woodland, found that breeding productivity was positively related to the area of ground free of grasses, and the amount of box bark, but negatively to the shrub density. Brown Treecreepers feed both on the ground and on trunks and large branches of eucalypts; boxes are a group of fibrous barked eucalypts.

High levels of nest predation, and relative food shortages, probably contribute to the area-sensitivity of Eastern Yellow Robins (*Eopsaltria australis*) and Hooded Robin (*Melanodryas cucullata*) in northern New South Wales (Fitri and Ford, 1997, 2003a, b; Zanette, 2000; Zanette and Jenkins, 2000; Zanette et al., 2000; Debus, 2006a, b). Thus, both isolation, through interrupted dispersal, and poor habitat quality may lead to losses of treecreepers and robins from patches long after the initial habitat loss.

Our aim in this paper is to incorporate a temporal perspective into the spatial and local perspectives of studies on the Brown Treecreeper and Hooded Robin. Specifically we shall test the following predictions:

- (1) Both species will continue to be lost from vegetation remnants in northern New South Wales.
- (2) These losses will be more evident in landscapes where remnant vegetation is poorly connected.
- (3) Losses of Brown Treecreepers will be more evident in sites that offer poor foraging sites.

We shall also consider the alternative hypotheses that ongoing species loss is the result of drought, climate change or the presence of Noisy Miners.

## 2. Methods

### 2.1. Study area and survey methodology

The study area is part of the Northern Tablelands Bioregion of north-eastern New South Wales, within a radius of 40 km of Armidale (Walters et al., 1999). It spans the Great Dividing Range, with altitude ranging from 750 to 1100 m. Vegetation in the central and eastern part of the region was mostly cleared in the 19th century with almost no clearing since the start of the study. Less than 10% of intact woodland remains in this eastern region, mostly in fairly isolated patches. In the late 1970s there was extensive mortality of trees in paddocks and remnants – “eucalypt dieback”

(Lowman and Heatwole, 1992), leading to further tree decline. Over the last two decades there has been some fencing of remnants to exclude grazing by livestock and planting of small patches or corridors of native vegetation. Two larger remnants were converted from state forest, where livestock grazing is permitted, to nature reserves, in which there are no livestock. In the far south east of the region there are extensive gorges with large areas of continuous eucalypt forest, typically with dense shrubs, though such habitat appears to be unsuitable for Brown Treecreepers and Hooded Robins (Walters et al., 1999). Thus, patches of suitable woodland on the fringes of this forested area may still be functionally isolated. The western side of the region has more native woodland vegetation, which tends to be structurally well-connected.

In this study, we use the term 'site' to refer to a remnant or discrete part of more extensive habitat in which a territory or group of territories of the target species has occurred sometime during the study. The earlier studies searched the region broadly to identify occupied sites. The follow-up studies of VAJD, HAF and SJSJ from 1999 onwards specifically searched previously occupied territories in these sites. Both species are highly detectable in eucalypt woodlands. Brown Treecreepers are vocal during the breeding season (Cooper and Walters, 2002a) and Hooded Robins are conspicuous, especially the black and white males, as they pounce from low perches onto the ground (Fitri and Ford, 2003a). Cooper and Walters (2002a) searched sites that were slightly larger than the 4.4 ha mean territory size of Brown Treecreepers for 1 h, when comparing landscape and habitat of occupied and unoccupied sites. In 1999 and 2007–2008 we spent from 40 to 60 min searching each known territory. If the target species was not found in any territory at a site, the area around the territories was searched for a further 60 min.

## 2.2. Study species and presence/absence surveys

HAF started a long-term study of birds in eucalypt woodlands in 1977, with an emphasis on habitat degradation from 1979 (e.g. Ford and Bell, 1982) and habitat fragmentation from 1980 (e.g. Howe, 1984; Barrett et al., 1994).

### 2.2.1. Brown Treecreeper

Brown treecreepers are the largest treecreeper (c 30–36 g) and forage on the ground or on tree trunks and large branches (Noske, 1985; Higgins et al., 2001). They inhabit woodlands and mallee (scrubby eucalypt woodland) in inland eastern Australia, being scarce east of the Great Dividing Range. They are facultative cooperative breeders, with breeding pairs frequently assisted by helpers, in the study area almost always males (Noske, 1991; Doerr and Doerr, 2006, 2007). Individuals may also assist in the breeding attempts of neighbouring groups. Young males remain in the parental territory or disperse to nearby territories, whereas females disperse more widely, within a remnant or to neighbouring remnants. They nest in tree hollows, experiencing high nest success relative to open-nesting small passerines in woodlands (Noske, 1991; Doerr and Doerr, 2006).

The authors surveyed Brown Treecreepers in remnants in the study area over several decades. Noske (1985) studied Brown Treecreepers at Wollomombi, c 40 km east of Armidale in the late 1970s, but the species disappeared from this site in the early 1980s. JRW searched numerous remnants up to 40 km east and west of Armidale in 1992. As early as 1992, he found that some groups in the eastern part of the region consisted only of males (Walters et al., 1999). Brown Treecreepers were studied in detail in 1995 (Walters et al., 1999), and in 1996–1998 (Cooper et al., 2002; Cooper and Walters, 2002a), expanding the number of groups and remnants monitored. Cooper and Walters (2002a) found that sites in the western part of the region were structurally

well-connected, whereas those in the east were isolated. CBC translocated females to some groups that consisted only of males in 1996–1998, with follow-up surveys by SJSJ in 1999. Some females stayed in more isolated sites and even bred successfully (Cooper and Walters, 2002b). In contrast, females translocated to structurally well-connected sites soon left them. VAJD monitored most sites in 1999 and a few sites in 2000–2002. HAF surveyed almost all sites in 2007, 2008 and/or 2009, noted the presence of the smaller and competitively subordinate White-throated Treecreeper (*Cormobates leucophaeus*).

One site where the species occurred, Imbota Nature Reserve (previously Eastwood State Forest) has been the location of ongoing research since 1978 by HAF and his students, including censuses in 1978, 1979, 1981 and 1988–1993 (Ford and Bell, 1982; Ford et al., 1985, Ford unpublished). While conducting research on other bird species from 1990 onwards, HAF and SJSJ noted when and where they saw Brown Treecreepers. Some of the eastern sites were also surveyed by Templeton (2001) in 2001 for a range of species, including both Brown Treecreepers and Hooded Robins.

### 2.2.2. Hooded Robin

Hooded Robins are fairly large robins (c 20 g), which forage primarily by pouncing from a low perch onto the ground (Fitri and Ford, 2003a). They are the most widespread Australian robin, occurring throughout much of the mainland, but being rare near the coast and east of the Great Dividing Range. They inhabit a wide variety of eucalypt, acacia and other woodlands and shrublands, and may sometimes occur in landscapes where trees and large shrubs are scarce (Higgins and Peter, 2002). They build open nests in trees and shrubs and suffer high levels of nest predation (22% nest success – Fitri and Ford (2003b)), typical of many open-nesting birds in eucalypt woodland (Ford et al., 2001). Extra males sometimes help nesting pairs.

HAF, SJSJ and others have studied Hooded Robins near Armidale over several decades. Bell (1984) studied a group of Hooded Robins at Wollomombi in the late 1970s, but they have not been seen there since. Fitri studied Hooded Robins within the study area in the early 1990s (Fitri and Ford, 1997). HAF had seen Hooded Robins in four sites previous to Fitri's study but could not find them in 1991 (Fitri and Ford (1997)). SJSJ searched remnants east and north of Armidale in 2005 and 2006 for Hooded Robins and failed to find them in any of the known sites, though he did find three new groups in two previously unsurveyed sites. HAF searched for Hooded Robins in all 11 of Fitri's sites in 2007 and 2008.

HAF also recorded the presence of all bird species at each site that he visited in 2007 and 2008, especially seeking any other robin species. He also estimated numbers of Noisy Miners, noting whether any parts of the site were dominated by this aggressive species.

## 3. Results

### 3.1. Brown Treecreeper

Brown Treecreepers were surveyed more than once in a total of 21 sites, nine in the more fragmented eastern region and 12 in the better-connected western region. Fourteen sites had been surveyed at least once by 1992, and all sites had been surveyed at least once by 1995/1996 (Table 1, Fig. 1a and b). However, by 1995 treecreepers had already gone from one site out of seven in the western region and three sites out of seven in the eastern region, including Noske's (1979) site in the far east, where Brown Treecreepers occurred until the early 1980s. Most of the 1995 sites were still occupied through 1996–1998 (Table 1). Many of



**Table 1**

Locations at which Brown Treecreepers were detected near Armidale. 1 indicates present in that year (s), 0 indicates site checked and Brown Treecreepers not recorded, blank indicates not checked.

Site name	Latitude	Longitude	Site area (ha)	C 1980	1992	1995	1996–1998	1999	2007–2009	
<i>Eastern region</i>										
Wollomombi	30 31.5	152 1.25	160	1	0	0	0		0	WTT
Blue hole	30 36	151 47.5	100	1	1	1	1	1	0	WTT
Yina	30 30.5	151 45	140	1	1	1	1 <sup>a</sup>	0	0	WTT
Pine forest	30 29.5	151 43.5	80			1	1	0	0	
Dangars falls	30 40.5	151 43.3	140	1	1	1	1 <sup>a</sup>	0	0	WTT
UNE	30 29	151 39	20	1	0	0	0	0	0	
Newholme	30 25	151 38.7	100	1	0				0	WTT
Imbota	30 34.8	151 42.8	270	1	1	1	1 <sup>a</sup>	1	0	WTT
Rockvale road	30 29.3	151 41.4	60				1	0		
<i>Western region</i>										
Fardell's corner	30 31.8	151 31.7	75			1	1 <sup>a</sup>	0	0	
Blackfellows	30 30.2	151 31	20		1	0			0	WTT
Uralla goldfield	30 37.8	151 28.3	180		1	1	1 <sup>a</sup>	1	0	WTT
Milsons bridge	30 29	151 25.5	60		1	1	1	1	1	WTT
S Yarrowyck X	30 29	151 21.8	150			1	1	1	1	WTT
N Yarrowyck X	30 28	151 22	65			1	1	1	1	WTT
Mount View	30 28	151 20	50		1	1	1	1	1	WTT
Double J	30 28	151 18.5	70		1	1	1 <sup>a</sup>	1	0	WTT
Morweena	30 27.5	151 16	80	1	1	1	1	1	1	
Gwydir park	30 26.3	151 14	170	1	1	1	1 <sup>a</sup>	1	1	WTT
Tullimba	30 28	151 12	70			1	1	0	1	WTT
Lansdale	30 27	151 10.4	100			1	1	1		

WTT indicates presence of White-throated Treecreepers in the site during 2007–2008 surveys.

<sup>a</sup> Indicates that at least one female was translocated to this site in 1998.

these sites even received translocated females in 1998, some of which bred at sites that previously had males only (Cooper and Walters 2002b). However, by 1999 Brown Treecreepers had apparently disappeared from two more sites in the western region and four additional sites in the eastern region (Table 1). By 2007–2009 no Brown Treecreepers were found in any of the nine sites in the fragmented eastern region, although they were known to be present in two of these until at least 2001 (Table 1, Fig. 1c). The species had apparently gone from an additional two western sites in which multiple territories had been occupied in 1999. A single, highly mobile, bird was seen at Tullimba in 2008, where the species was not seen in 1999. This is the only case of the species being detected in a population that was thought to have gone locally extinct before 2007. Thus, only seven out of 12 sites in the well-connected western region are still occupied. Furthermore, three of these sites (Milson Bridge, N Yarrowyck Crossing and Mount View) were thought to support only single groups of birds by 2007–2008 and one only a single individual in 2009. Even the sites with several treecreeper groups now have vacant territories, with only five out of 14 territories closely monitored in 1998 still being occupied in 2009.

Ten years later, Brown Treecreepers had therefore gone from significantly more sites occupied in 1998 from the eastern than western region of the study area ( $p = 0.042$ , exact test). They had also gone from significantly more eastern sites that have been occupied at any time between 1980 and 1998 ( $p = 0.014$ , exact test).

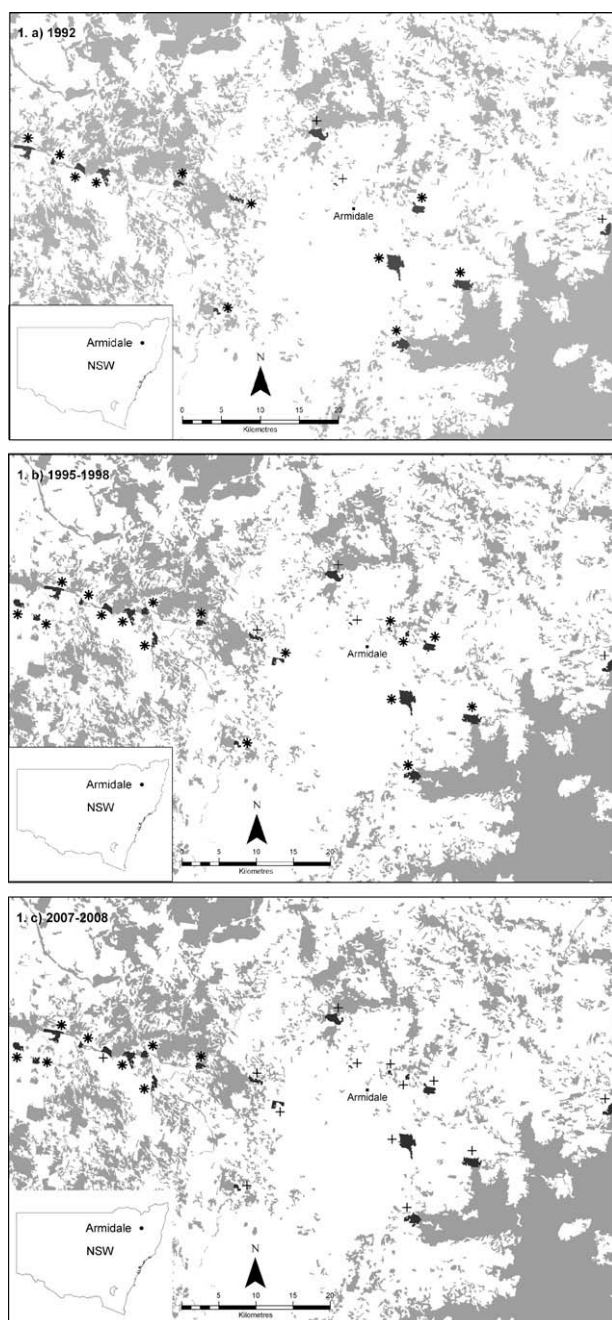
The Brown Treecreepers at Imbota Nature Reserve have been followed for longer than other populations. Censuses in 1978–1981 indicated a density of c. 0.1 birds/ha (Ford and Bell 1982; Ford et al. 1985), which in 270 ha would have meant about 10 groups. There were at least three remaining groups in 1992–1995, although by 1998 only one had a female. Females were translocated to the other groups in late 1998, but by late 1999, there was only one group left, where the species was seen regularly until 2001. Less complete information is available for Yina Nature Reserve. This 140 ha remnant had c. 0.3 birds/ha in 1981 (Ford

et al. 1985), perhaps 15 groups. There were five groups in 1992–1995, though three only had males. Females were translocated in late 1998. However, no Brown Treecreepers were found there in 1999 or 2001 by SJS, who visited the site regularly in those years, nor have any been seen since. Cattle and horses grazed both Imbota and Yina Nature Reserves when they were State Forests, but this ceased in 1999. Brown Treecreepers were extinct in both within about 3 years of the change in land-use. This last Brown Treecreeper group at Imbota occurred mainly in neighbouring private land, in which grazing also ceased in 2001 and understorey, herbs and grasses re-established. A number of trees with hollows were also felled there.

CBC measured habitat variables in 26 closely monitored territories in 1998 (Cooper and Walters 2002a). Only seven of these were still occupied in 2007–2009. Occupied territories had significantly more box trees ( $t$  test,  $p = 0.04$ ) than vacated territories. There were no significant differences between occupied and vacated territories in grass cover, bare ground, logs or hollows in 1998, though as shown at Imbota and Yina Nature Reserves, changing land uses at some sites may have altered these parameters over the last 10 years.

### 3.2. Hooded Robins

Hooded Robins were known to be present in six sites in the eastern region and five sites in the western region in 1992 (Table 2, Fig. 2a). In addition, they had gone from four other sites in the eastern region between 1980 and 1992, including the well-studied Imbota Nature Reserve (Fitri and Ford 1997). They still occurred in four eastern sites in 2001 (Templeton 2001), but were not found in these sites in 2005 nor 2007 (Table 2, Fig. 2b). In 2006 a group was found in private property and two groups were found in an exotic Monterey Pine (*Pinus radiata*) plantation, north of Armidale. In the western region, four of the five known populations appeared to have gone locally extinct by 2007–2008. Finally, none of four sites from which the species had gone before 2007, was recolonised by 2007–2008.



**Fig. 1.** Distribution of known extant (\*) and extinct (+) populations of Brown Treecreepers in: (a) 1992; (b) 1995; (c) 2007–2008.

### 3.3. Other woodland birds

Noisy Miners occurred in low numbers in most sites or only in parts of a site in 2007 and 2008. From 12 to 40 species of woodland bird (mean of 23 species), other than the target species, Noisy Miners or waterbirds, were recorded per survey. Sites with Brown Treecreepers had a mean of 25.3 species and those without had 20.8 species, which did not differ significantly ( $t = 1.15$ ,  $p > 0.05$ ). White-throated Treecreepers or one or more species of robin (Table 1 and 2) were recorded at 15 and 13 out of the 18 sites visited in 2007–2008. Only Fardell's Corner was dominated by Noisy Miners and had only 12 woodland bird species, with no treecreepers or robins. Noisy Miners dominate the south-west corner of Imbota, but have done so since at least the 1980s, with minimal expansion of their range.

## 4. Discussion

### 4.1. Ongoing loss from sites

Brown Treecreepers appear to have gone extinct in a total of 13 local sites (62% of known local populations) over 30 years, nine of these over the last 10 years. Although some of these “populations” consisted of single groups and occasionally only of males when discovered, we documented two populations of 10–15 groups going extinct over about 20 years. Four of the remaining seven populations only contain single groups now, suggesting they too may disappear soon. Even in the two “healthy” sites, many previous territories are now vacant. Hooded Robins have gone from all but one of the 15 previously occupied sites near Armidale, some in the 1980s, but mostly since 2000. Other pairs or groups of both species could occur in unsurveyed private land around Armidale. In addition, it is possible that both species were overlooked in some sites. However, only in one site from which a species was believed to have gone in earlier surveys was it rediscovered in 2007–2009 and then there was only a single individual. We are especially confident that both species have gone from the well-studied Imbota and Yina Nature Reserves, which previously held large populations of Brown Treecreepers. It seems likely that both species will show further local losses and may ultimately become extinct in the whole region.

The losses that we found in a fragmented landscape are not unique to our region. Reid (1999) identified both Brown Treecreepers and Hooded Robins as declining woodland birds and Saunders (1989) noted the extinction of Hooded Robins and Rufous Treecreepers (a sibling species of the Brown Treecreeper) in a well-studied district of the Western Australian Wheatbelt. Both species appear sensitive to patch size and isolation (Seddon et al. 2003; Watson et al. 2005; Maron and Lill 2006). Most of the native vegetation in the Armidale area was cleared over 100 years ago, and virtually none since 1980. Thus, the losses we observed may be due to the delayed effects of habitat fragmentation, i.e. extinction debt, or be due to habitat change. The local and regional loss of bird species from eucalypt woodlands in south-western (Saunders 1989) and south-eastern Australia (Ford et al. 2001), and the loss of an average of nine bird species from eucalypt forest remnants in Victoria over 22 years (MacHunter et al. 2006) indicate that a large number of birds in eucalypt woodland may be suffering the effects of extinction debt.

### 4.2. Extinction debt due to habitat fragmentation

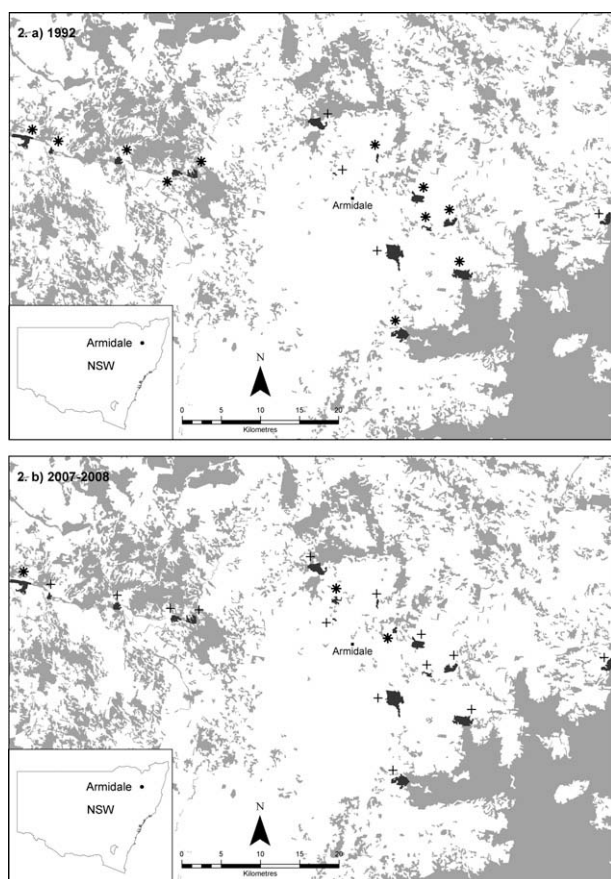
As we predicted, local populations of Brown Treecreepers were more likely to go extinct in the more fragmented eastern part of the region than in the better-connected western part. Indeed, the species has now contracted some 60 km westwards in the region. There is substantial evidence that Brown Treecreepers suffer poor dispersal in fragmented landscapes. Walters et al. (1999) argued that more male-only groups of Brown Treecreepers east than west of Armidale indicated that female dispersal was disrupted in the former. Females translocated to males in isolated sites were more likely to stay than those translocated to better-connected sites (Cooper and Walters 2002b). Some even bred, a few successfully. This suggests that females were absent from isolated sites because they were unable to reach them rather than because they rejected them due to poor habitat. Each successive local extinction means that all remaining populations become more isolated, hastening their demise (Radford and Bennett 2004).

Australian treecreepers, as hollow-nesters, experience high nest success (Higgins et al. 2001). In our study area in the late 1990s, Brown Treecreepers produced an average of 1.33 fledglings/

**Table 2**

Locations at which Hooded Robins were detected near Armidale. 1 indicates present in that year (s), 0 indicates site checked and Hooded Robins not recorded, blank indicates not checked. Other robins – EYR – Eastern Yellow Robin, SRO – Scarlet Robin, FRO – Flame Robin, JWJ – Jacky Winter, indicates these species were present in the site during 2007–2008 surveys.

Site name	Latitude	Longitude	C 1980	1992	2001	2005–06	2007–08	Other robins
<i>Eastern region</i>								
Wollomombi	30 31.5	152 1.25	1	0		0	0	EYR, SRO
Blue hole	30 36	151 47.5		1	1	0	0	SRO, EYR
Gara reserve	30 37.5	151 47.5		1	1	0	0	SRO
Strathaven	30 33.2	151 46.3		1	0	0	0	SRO
Yina	30 30.5	151 45		1	1	0	0	SRO, EYR
Pine forest	30 29.5	151 43.5				1	1	SRO, EYR
Dangars falls	30 40.5	151 43.3		1	1	0	0	SRO
Imbota	30 34.8	151 42.8	1	0	0	0	0	EYR, SRO
Walking track	30 28	151 42		1			0	
UNE	30 29	151 39	1	0			0	
Newholme	30 25	151 38.7	1	0			0	EYR, SRO, FRO
Kirby road	30 28	151 38				1	1	
<i>Western region</i>								
Hillcrest	30 29	151 26.5		1			0	JWJ
Milsons bridge	30 29	151 25.5		1			0	EYR
N Yarrowyck X	30 28	151 22		1		0	0	JWJ
Morweena	30 27.5	151 16	1	1		0	0	JWJ
Gwydir park	30 26.3	151 14	1	1		1	1	EYR, JWJ



**Fig. 2.** Distribution of known extant (\*) and extinct (+) populations of Hooded Robins in: (a) 1992 and (b) 2007–2008.

group/year (Cooper et al. 2002), similar to Noske's (1991) figures of 1.36 fledglings/group/year from a study area about 100 km north of ours. Cooper et al. (2002) found no evidence that patch size or isolation influenced breeding success or productivity. Brown Treecreepers show high adult survival: 79% for females (Cooper et al., 2002), 78% (Noske, 1991) and 74% (Doerr and Doerr, 2006) for both sexes from a site in central New South Wales. Noske or Cooper did

not calculate fledgling survival to the next breeding season, but Doerr et al. (2006) found that 58% of fledglings survived to dispersal age. Cooper et al. (2002) found that adult female survival was significantly affected by patch size and isolation (58% is small, isolated sites, 73% in small, connected sites and 90% and 94% is large connected and isolated sites respectively). These figures suggest that 0.39 new female recruits are produced annually on average in our region (using fledgling survival from Doerr et al., 2006). This is adequate to replace female mortality in all except small, isolated sites. Hence, there is good evidence that fragmentation leads to loss of local populations, principally due to isolation, but with small patch size contributing.

There is less information on the dispersal ability of Hooded Robins, or on the effect of fragmentation on dispersal. Maron and Lill (2006) found that isolation negatively influenced patch occupancy but it did not recolonise any sites from which it had been lost. However, Hooded Robins venture well into open pasture to forage (Fitri and Ford, 2003a) and are common in very open vegetation in inland Australia (Higgins and Peter, 2002). One Eastern Yellow Robin moved 7 km between Imbota and Yina Nature Reserves and back, and a translocated bird moved daily among remnants separated by more than 1 km (Debus and Ford, pers. obs.). The local matrix contains scattered trees and patches of woodland, which may aid the movement of robins. So, the Hooded Robin may be a better disperser than the Brown Treecreeper and dispersal problems may not be the cause of its decline.

Robins, as with most open-nesting birds in eucalypt woodland, suffer high rates of nest predation (Ford et al., 2001). Fitri and Ford (2003b) found that 22% of Hooded Robin nests with eggs were successful and, over two years groups reared an average of 0.72 fledglings per year near Armidale. They suggested that Hooded Robin populations were not sustainable, but had no data on adult or juvenile survival. Zanette (2000) calculated 72% adult female survival of Eastern Yellow Robins in four sites about 50 km west of Armidale, with 36% of independent young surviving to the next breeding season. Comparable figures for Hooded Robins indicate an annual decline of 15% annually (intrinsic rate of increase  $\lambda = 0.85$ ). Zanette's Yellow Robins, which produced 1.78 fledglings/group/year and 1.37 independent young/group/year, were also just below sustainability ( $\lambda = 0.96$ ). Debus (2006b) also found Eastern Yellow Robins at Imbota NR to be unsustainable ( $\lambda = 0.83$ ).

Hence, classic extinction debt, by random losses of sub-populations, provides an adequate explanation for the decline of these



two woodland bird species. However, whereas interrupted dispersal plays a major role in Brown Treecreepers, with females being lost from small, isolated sites; chronically low production of young may be the driving force in Hooded Robins. Tilman et al. (1994) predicted that superior competitors are likely candidates for extinction debt. Our two species are the largest treecreeper (out of three species) and largest robin (out of six species) that breed regularly in the region. They also dominate their relatives aggressively (treecreepers – Noske, 1979; Doerr and Doerr, 2006, robins – Fitri and Ford, 1998).

#### 4.3. Extinction debt due to changes in habitat quality

Groups of Brown Treecreepers in the well-connected western region are also starting to show the same pattern that was shown in the fragmented eastern region in the early 1990s. Some populations have gone extinct, others are only single groups, and territories are now vacant even in the best two sites. Poor dispersal provides a less satisfactory explanation for the population declines and losses in this region. Differences in habitat quality may also affect the probability of occurrence at a site, adult or immature survival rates and reproductive success and productivity.

Brown Treecreepers select habitat at several levels. They are more frequent in woodland with red gum (*E. camaldulensis*) and box trees (Major et al., 2001; Antos and Bennett, 2005), and in shrubbier *belah* and *buloke* (*Casuarina* and *Allocasuarina* spp.) woodlands (Maron and Lill, 2006). Brown Treecreepers spend about half of their time foraging on the ground. Hence, the structure of ground and understorey vegetation, which is affected by livestock grazing, may influence whether they occur in a site. The species was found mostly in partly cleared grazing land near Armidale (Noske, 1979), and is more common in lightly than in heavily grazed sites (James, 2003). Martin and Possingham (2005) found highest densities under moderate rather than high or no grazing, which is also what “experts” predicted (Martin et al., 2005). Maron and Lill (2005) found that Brown Treecreepers were less abundant in ungrazed pasture with introduced weeds and grasses than in ungrazed or grazed native pasture. Maron and Lill suggested that a ground layer consisting of a cryptogamic crust with fine leaf litter and scattered grass clumps was most favourable for Brown Treecreepers. The species is also more abundant where there is more coarse woody debris, which may harbour their invertebrate prey (Mac Nally et al., 2001, 2002).

Walters et al. (1999) found no difference in the time spent foraging by Brown Treecreepers between the more and less connected parts of our study area, suggesting that they did not differ in quality. However, treecreepers fed more on stringybarks (mostly *E. caliginosa*) in fragmented sites, which could indicate poor quality foraging as this tree species occurs on poor, rocky soils. Maron and Lill (2006) found that Brown Treecreepers fed less on the ground where there were dense weeds or grass.

While Cooper and Walters (2002b) rejected habitat degradation as an explanation specifically for the lack of breeding females in isolated patches relative to connected patches, they conceded that habitat degradation could adversely affect the species in both isolated and connected sites and could account for the loss of Brown Treecreepers anywhere in the region. Furthermore, they collected their data before many of the population losses occurred, particularly those in the western region of our study area. Brown Treecreepers nest in tree hollows and Cooper and Walters (2002a) found that although habitat fragmentation best predicted patch occupancy near Armidale ( $r^2$  up to 37%) in 1998, the number of tree hollows also contributed significantly to their presence in a site ( $r^2$  of 19% when isolated sites were excluded).

Cooper et al. (2002) did not measure whether habitat quality may influence breeding success or survival of Brown Treecreepers.

However, they suggested that it could be important, but operating at the landscape scale rather than the remnant scale. In central New South Wales, Doerr et al. (2006) found that Brown Treecreeper groups produced more fledglings in sites with low shrub density, moderately low levels of grassy ground cover (25–35%) and more foraging substrate (surface area of box bark), and produced more independent young where there was more available food. Doerr et al. suggested that moderate grazing or appropriate fire regimes could help maintain the relatively open understorey and ground that promoted reproductive success. So, while heavy grazing could degrade food resources, completely excluding grazing by livestock, as has occurred over the last 10 years at Imbota and Yina NRs, could allow shrub density and ground cover to increase and be detrimental to the species. Many territories monitored by Cooper et al. (2002) in the late 1990s are now vacant, with those still occupied having a higher density of box trees than vacated territories. This suggests that in sites with many groups, poorer quality territories may be vacated first. When only a few groups remain, problems with dispersal and random fluctuations may become important. Firewood collection is also an ongoing activity in the study area, which could reduce densities of nest hollows and coarse woody debris. However, the ground layer, or abundance of logs and hollows at the time of surveying in 1998, did not differ between currently occupied or vacant territories, though changes in land use may have led to subsequent changes in these – notably a thickening of vegetation.

##### 4.3.1. Hooded Robin

Hooded Robins have a broad distribution occupying open, almost treeless areas through to woodlands (Higgins and Peter, 2002). Templeton (2001) found the species in sites with short grass and many saplings. They are more common in lightly than heavily grazed sites (James, 2003). Maron and Lill (2005) found that Hooded Robins avoided sites with exotic grasses, pounced more but gleaned less in weedy sites than in grazed sites, and perched lower in grazed sites (Maron and Lill, 2005). Antos et al. (2008) found that Hooded Robins foraged in sites with low tree density and abundant small, fallen timber. Habitat structure influences breeding success of other robins. Debus (2006b) found that Eastern Yellow Robins selected breeding sites with more rough-barked saplings, acacias and other shrubs, and their breeding success was positively correlated with these variables. Hooded Robins occupy much more open habitat, but breeding territories may include clumps of understorey or sapling eucalypts, which are used for nesting (Sullivan, 1993; Fitri and Ford, 2003b).

Zanette et al. (2000) found that ground invertebrates were less abundant in small than in large remnants 50 km west of Armidale. This slightly reduced the rate at which male Yellow Robins fed their mates while breeding, and also the size of prey brought to nestlings. However, any effect of food on breeding success was overwhelmed by predation.

We conclude that a reduction in the quality of habitat in the region, such as altered grazing by livestock and recovery of herbaceous vegetation, or loss of logs and hollows by firewood collection, may have had a negative impact on both of our species. However, we need more information on how habitat influences survival or reproductive success of these and other woodland birds.

#### 4.4. Other causes for decline and local extinction

Several other factors could contribute to local loss and regional decline of our species, such as drought, climate change and increases in Noisy Miners. The years 2001–2007 were drier than the long-term average across much of eastern and southern Australia, leading to substantial declines of many bird species, even in large tracts of native vegetation (Mac Nally et al., 2009). How-



ever, Armidale had an average rainfall of 739 mm for these years, only slightly below the long-term average rainfall of 790 mm ([www.bom.gov.au/climate/data/weather-data.shtml](http://www.bom.gov.au/climate/data/weather-data.shtml)). Australia has experienced increasing temperatures and declining rainfall towards the end of the 20th century, which have influenced the distribution of some bird species (Olsen, 2007). Brown Treecreepers are widespread in inland eastern Australia, and Hooded Robins occur across Australia (Barrett et al., 2003). The climate in their core distributions is both hotter and drier than near Armidale, which is cooler and wetter than almost anywhere that both species occur. A spread in range eastwards might have been predicted under recent climate change. Instead, both species have retreated westwards by 60–80 km. So, we consider it improbable that drought or climate change has contributed to the decline of our species around Armidale.

Noisy Miners now dominate only one site from which Brown Treecreepers have gone extinct (Fardell's Corner) and may have caused the species' extinction there. Noisy Miners occur in most sites, including those where our species still occur, but they are patchy or at low density, and many other woodland bird species, which are usually driven out by Miners, were recorded in 2007–2008. Therefore, we consider it unlikely that Noisy Miners were a major factor in local extinctions of our species.

#### 4.5. Conclusions and implications for conservation

Loss of woodland and forest birds and other organisms in fragmented landscapes, sometimes well after the intervening vegetation has been removed, is a well-known phenomenon. Our study is unusual because we have documented the progressive loss and regional decline of two species of woodland birds over 30 years. In addition, we have a good understanding of the ecological processes involved in the decline of one species. Local populations of Brown Treecreepers go through a sequence of vacation of territories, loss of females leading to male-only groups and final disappearance. This has been repeated throughout the region. A major reason for this is that females disperse from remnants and fail to find other isolated remnants. In the case of Hooded Robins, it appears to be poor recruitment and hence a lack of dispersers, rather than poor dispersal ability, that is the cause of local losses. It is also interesting that we are losing the largest and dominant species, whose smaller relatives are surviving well. This aspect needs to be studied. The loss of our species thus gives the appearance of payment of an extinction debt and we predict that regional extinction will be the result.

Brown Treecreepers are now declining within and disappearing from sites that are well-connected and Hooded Robins show chronically low reproductive success. This suggests that habitat quality may also play a part in local extinctions. Brown Treecreepers avoid ungrazed sites with dense ground vegetation, and produce fewer young in sites with greater shrub and ground cover. Hooded Robins may require a combination of open ground with patches of saplings to forage and nest successfully. It is possible that removal of livestock from sites that have become national parks, combined with a reduction in natural disturbance, has reduced grazing pressure generally, and allowed an increase in shrub and ground vegetation, which may reduce the foraging efficiency of ground-feeding birds.

It is likely that many other eucalypt woodland birds are following similar trajectories towards regional extinction and this pattern is being repeated in woodlands and forests around the world. Enlarging and connecting remnants with corridors may help to maintain populations of species that, like Brown Treecreepers, are poor dispersers. However, it may be inadequate alone. We may also need to understand how the quality of the habitat influences foraging ability, reproductive success and local desertion of

territories and sites. Managers may need to reintroduce grazing and/or fire at appropriate levels and times to conserve ground-foraging birds.

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#### References

- Andr en, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71, 355–366.
- Antos, M.J., Bennett, A.F., 2005. How important are different types of temperate woodlands for ground-foraging birds? *Wildlife Research* 32, 557–572.
- Antos, M.J., Bennett, A.F., White, J.G., 2008. Where exactly do ground-foraging woodland birds forage? Foraging sites and microhabitat selection in temperate woodlands of southern Australia. *Emu* 108, 201–212.
- Barrett, G.W., Ford, H.A., Recher, H.F., 1994. Conservation of woodland birds in a fragmented rural landscape. *Pacific Conservation Biology* 1, 245–256.
- Barrett, G.W., Silcocks, A., Barry, S., Cunningham, R., Poulter, R., 2003. *The New Atlas of Australian Birds*. RAOU, Melbourne.
- Bell, H.L., 1984. A note on communal breeding and dispersal of young of the Hooded Robin *Petroica cucullata*. *Emu* 84, 243–244.
- Brooks, T.M., Pimm, S.L., Oyugi, J.O., 1999. Time lag between deforestation and bird extinction in tropical forest fragments. *Conservation Biology* 13, 1140–1150.
- Castelletta, M., Sodhi, N., Subaraj, R., 2000. Heavy extinctions of forest avifauna in Singapore: lessons for biodiversity conservation in Southeast Asia. *Conservation Biology* 14, 1870–1880.
- Christiansen, M.B., Pitter, E., 1997. Species loss in a forest bird community near Lagoa Santa in southeastern Brazil. *Biological Conservation* 80, 23–32.
- Connor, E.F., McCoy, E.D., 1979. The statistics and biology of the species-area relationship. *American Naturalist* 113, 791–833.
- Cooper, C.B., Walters, J.R., 2002a. Independent effects of woodland loss and fragmentation on Brown Treecreeper distribution. *Biological Conservation* 105, 1–10.
- Cooper, C.B., Walters, J.R., 2002b. Experimental evidence of disrupted dispersal causing decline of an Australian passerine in fragmented habitat. *Conservation Biology* 16, 471–478.
- Cooper, C.B., Walters, J.R., Ford, H.A., 2002. Effects of remnant size and connectivity on the response of Brown treecreepers to habitat fragmentation. *Emu* 102, 249–256.
- Debus, S.J.S., 2006a. Breeding-habitat and nest-site characteristics of Scarlet Robins and Eastern Yellow Robins near Armidale, New South Wales. *Pacific Conservation Biology* 12, 261–271.
- Debus, S.J.S., 2006b. Breeding and population parameters of robins in a woodland remnant in northern New South Wales, Australia. *Emu* 106, 147–156.
- Diamond, J.M., 1975. Assembly of species communities. In: Cody, M.L., Diamond, J.M. (Eds.), *Ecology and Evolution of Communities*. Harvard University Press, Cambridge, Massachusetts, pp. 342–444.
- Doerr, E.D., Doerr, V.A.J., 2006. Comparative demography of treecreepers: evaluating hypotheses for the evolution and maintenance of cooperative breeding. *Animal Behaviour* 72, 147–159.
- Doerr, E.D., Doerr, V.A.J., 2007. Positive effects of helpers on reproductive success in the brown treecreeper and the general importance of future benefits. *Journal of Animal Ecology* 76, 966–976.
- Doerr, V.A.J., Doerr, E.D., Jenkins, S.H., 2006. Habitat selection in two Australian treecreepers: what cues should they use? *Emu* 106, 93–103.
- Fahrig, L., 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61, 603–610.
- Fitri, L.L., Ford, H.A., 1997. Status, habitat preferences and social organization of the Hooded Robin *Melanodryas cucullata* in the Northern Tablelands of New South Wales. *Australian Bird Watcher* 17, 142–155.
- Fitri, L.L., Ford, H.A., 1998. Aggression among Hooded Robins *Melanodryas cucullata* and other birds. *Corella* 22, 24–29.
- Fitri, L.L., Ford, H.A., 2003a. Foraging behaviour of Hooded Robins *Melanodryas cucullata* in the Northern Tablelands of New South Wales. *Corella* 27, 61–67.
- Fitri, L.L., Ford, H.A., 2003b. Breeding biology of Hooded Robins *Melanodryas cucullata* in New England, New South Wales. *Corella* 27, 68–77.
- Ford, H.A., Bell, H.L., 1982. Density of birds in eucalypt woodland affected to varying degrees by dieback. *Emu* 82, 202–208.
- Ford, H.A., Bridges, L., Noske, S., 1985. Density of birds in eucalypt woodland near Armidale, north-eastern New South Wales. *Corella* 9, 97–107.

- Ford, H.A., Barrett, G.W., Saunders, D.A., Recher, H.F., 2001. Why have birds in the woodlands of southern Australia declined? *Biological Conservation* 97, 71–88.
- Grey, M.J., Clarke, M.F., Loyn, R.H., 1998. Influence of the noisy miner *Manorina melanoccephala* on avian diversity and abundance in remnant grey box woodland. *Pacific Conservation Biology* 4, 55–69.
- Higgins, P.J., Peter, J.M., 2002. Handbook of Australian, New Zealand and Antarctic Birds. Pardalotes to Shrike-thrushes, vol. 6. Oxford University Press, Melbourne.
- Higgins, P.J., Peter, J.M., Steele, W.K., 2001. Handbook of Australian, New Zealand and Antarctic Birds. Tyrant-flycatchers to Chats, vol. 5. Oxford University Press, Melbourne.
- Howe, R.W., 1984. Local dynamics of bird assemblages in small forest fragments in Australia and North America. *Ecology* 65, 1585–1601.
- James, C.D., 2003. Response of vertebrates to fence-line contrasts in grazing intensity in semi-arid woodlands of eastern Australia. *Austral Ecology* 28, 137–151.
- Lowman, M.D., Heatwole, H., 1992. Spatial and temporal variability in defoliation of Australian eucalypts. *Ecology* 73, 129–142.
- Luck, G.W., 2002a. Determining habitat quality for the cooperatively breeding Rufous Treecreeper, *Climacteris rufa*. *Austral Ecology* 27, 229–237.
- Luck, G.W., 2002b. The habitat requirements of the Rufous Treecreeper (*Climacteris rufa*). 1. Preferential habitat use demonstrated at multiple spatial scales. *Biological Conservation* 105, 383–394.
- Luck, G.W., 2003. Differences in the reproductive success and survival of the Rufous Treecreeper (*Climacteris rufa*) between a fragmented and unfragmented landscape. *Biological Conservation* 109, 1–14.
- Mac Nally, R., Parkinson, A., Horrocks, G., Conole, L., Tzaros, C., 2001. Relationships between terrestrial vertebrate diversity, abundance and availability of coarse woody debris on south-eastern Australian floodplains. *Biological Conservation* 99, 191–205.
- Mac Nally, R., Horrocks, G., Pettifer, L., 2002. Experimental evidence for potential beneficial effects of fallen timber in forests. *Ecological Applications* 12, 1588–1594.
- Mac Nally, R., Bennett, A., Thomson, J., Radford, J., Unmack, G., Horrocks, G., Vesik, P., 2009. Collapse of an avifauna: climate change appears to exacerbate habitat loss and degradation. *Diversity and Distributions* 15, 720–730.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- MacHunter, J., Wright, W., Loyn, R.H., Rayment, D., 2006. Bird declines over 22 years in forest remnants in south-eastern Australia: evidence of faunal relaxation? *Canadian Journal of Forest Research* 36, 2756–2768.
- Major, R.E., Christie, F.J., Gowing, G., 2001. Influence of remnant and landscape attributes on Australian woodland bird communities. *Biological Conservation* 122, 47–66.
- Malanson, G.P., 2008. Extinction debt: origins, developments, and applications of a biogeographical trope. *Progress in Physical Geography* 32, 277–291.
- Maron, M., 2007. Threshold effect of eucalypt density on an aggressive avian competitor. *Biological Conservation* 137, 100–107.
- Maron, M., Lill, A., 2005. The influence of livestock grazing and weed invasion on habitat use by birds in grassy woodland remnants. *Biological Conservation* 124, 439–450.
- Maron, M., Lill, A., 2006. Interspecific variation in detection of bird-habitat relationships: declining birds in southern Australian woodlands. *Pacific Conservation Biology* 12, 301–312.
- Martin, T.G., Possingham, H.P., 2005. Predicting the impact of livestock grazing on birds using foraging height data. *Journal of Applied Ecology* 42, 400–408.
- Martin, T.G., Kuhnert, P.M., Mengersen, K., Possingham, H.P., 2005. The power of expert opinion in ecological models using Bayesian methods: impact of grazing on birds. *Ecological Applications* 15, 266–280.
- Metzger, J.P., Martensen, A.C., Dixo, M., Bernacci, L.C., Ribeiro, M.C., Teixeira, A.M.G., Pardini, R., 2009. Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. *Biological Conservation* 142, 1166–1177.
- Noske, R.A., 1979. Co-existence of three species of treecreepers in north-eastern New South Wales. *Emu* 79, 120–128.
- Noske, R.A., 1985. Habitat use by bark foragers of eucalypt forest. In: Keast, A., Recher, H.F., Ford, H.A., Saunders, D.A. (Eds.), *Birds of Eucalypt Forests and Woodlands: Ecology, Conservation and Management*. Surrey Beatty and Sons, Chipping Norton, NSW, pp. 193–204.
- Noske, R.A., 1991. A demographic comparison of cooperatively breeding and non-cooperative treecreepers (Climacteridae). *Emu* 91, 73–86.
- Olsen, P., 2007. *The State of Australia's Birds 2007. Birds in a Changing Climate. Supplement to Wingspan* 14, no 4.
- Olsen, P., Weston, M., Tzaros, C., Silcocks, A., 2005. *The State of Australia's Birds 2005. Woodlands and Birds. Supplement to Wingspan* 15, no 4.
- Possingham, H., Field, S.A., 2001. Regional bird extinctions and their implications for vegetation clearance policy. *Life Lines* 7, 15–16.
- Radford, J.Q., Bennett, A.F., 2004. Thresholds in landscape parameters: occurrence of the white-browed treecreeper *Climacteris affinis* in Victoria, Australia. *Biological Conservation* 117, 375–391.
- Radford, J.Q., Bennett, A.F., Cheers, G.J., 2005. Landscape level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation* 124, 317–337.
- Reid, J.R.W., 1999. Threatened and declining birds in the New South Wales Sheep-Wheat belt: 1. Diagnosis, characteristics and management. Consultancy report to NSW National Parks and Wildlife Service. CSIRO Wildlife and Ecology, Canberra.
- Robinson, D., Trail, B.J., 1996. Conserving woodland birds in the wheat and sheep belts of southern Australia. Royal Australasian Ornithologists Union conservation statement 10. *Wingspan* 6 (Suppl), 1–16.
- Saunders, D.A., 1989. Changes in the avifauna of a region, district and remnant as a result of fragmentation of native vegetation: the Wheatbelt of Western Australia. A case study. *Biological Conservation* 50, 99–135.
- Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of habitat fragmentation: a review. *Conservation Biology* 5, 18–32.
- Seddon, J.A., Briggs, S.V., Doyle, S.J., 2003. Relationships between bird species and characteristics of woodland remnants in central New South Wales. *Pacific Conservation Biology* 9, 95–119.
- Sullivan, D., 1993. The breeding and non-breeding behaviour of the Hooded Robin *Melanodryas cucullata* in Canberra, 1990–1991. *Australian Bird Watcher* 15, 99–107.
- Templeton, A.E., 2001. Distribution and behaviour of declining woodland birds in a fragmented and degraded rural landscape. BSc (Hons) thesis, University of New England.
- Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 1994. Habitat destruction and the extinction debt. *Nature* 371, 65–66.
- Walters, J.R., Ford, H.A., Cooper, C.B., 1999. The ecological basis of sensitivity of brown treecreepers to habitat fragmentation: a preliminary assessment. *Biological Conservation* 90, 13–20.
- Watson, J.E.M., Whittaker, R.J., Freudenberger, D., 2005. Bird community responses to habitat fragmentation: how consistent are they across landscapes? *Journal of Biogeography* 32, 1353–1370.
- Willis, E.O., 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecological Monographs* 44, 153–169.
- With, K.A., King, A.W., Jensen, W.E., 2008. Remaining large grasslands may not be sufficient to prevent grassland bird declines. *Biological Conservation* 141, 3152–3167.
- Woinarski, J.C.Z., McCosker, J.C., Gordon, G., Lawrie, B., James, C., Augusteyn, J., Slater, L., Danvers, T., 2006. Monitoring change in the vertebrate fauna of central Queensland, Australia, over a period of broad-scale vegetation clearance, 1973–2002. *Wildlife Research* 33, 263–274.
- Zanette, L., 2000. Fragment size and the demography of an area sensitive songbird. *Journal of Animal Ecology* 69, 458–470.
- Zanette, L., Jenkins, B., 2000. Nesting success and nest predators in forest fragments: a study using real and artificial nests. *Auk* 117, 445–454.
- Zanette, L., Doyle, P., Tremont, S.M., 2000. Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology* 81, 1654–1666.