Effects of mistletoe on diversity:
a case-study from southern New South Wales

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Abstract. The influence of mistletoe density on avian diversity has been noted previously, with several studies demonstrating a close positive relationship between the two variables. All previous work has been correlative, exploiting naturally occurring variation in mistletoe density, and hence unable to demonstrate a causative link between mistletoe density and avian richness. Here I compare the avifauna of two adjacent woodland remnants, one of which has had most mistletoe plants removed, but otherwise comparable in area, vegetation and grazing history. Ten-hour inventories were conducted in each remnant in both spring and summer, resulting in a total of 40 hours of censuses. Of the 71 species recorded overall, 52 were recorded from the treatment site (with reduced mistletoe density) and 61 species from the control site. Significantly more woodland-dependent species and species known to feed on mistletoe were recorded in the control site, while there was no significant difference for those species known to nest in mistletoe. These results broadly support the idea that mistletoe is a keystone resource, with mistletoe density having a significant positive effect on species richness. These findings reinforce previous correlative studies, and further highlight the importance of mistletoe in Australian woodlands and forests.

Introduction

Recently, mistletoes have been proposed to function as keystone resources in forests and woodlands throughout the world, having a disproportionately large effect on faunal community composition and structure (Watson 2001). They provide abundant nutritional and nesting resources for a diverse range of birds, mammals and insects, which may be especially important during droughts and other periods of scarcity. Moreover, mistletoes provide important nesting resources, both directly as highly favoured nest sites and indirectly via hollow formation (Watson 2001). Given the breadth of interactions between animals and mistletoes, changes in numbers of mistletoe can lead to concomitant changes in community structure. In many habitats, there is a positive relationship between mistletoe density and avian richness, such that areas with more mistletoe plants have higher species richnesses (Rice *et al.* 1981; Bennetts 1991; Turner 1991; Watson 1994; Bennetts *et al.* 1996).

Many Australian habitats appear to fit this general pattern. A broad range of birds and mammals have been recorded feeding on mistletoes (Reid 1986; Choate *et al.* 1987; Barker and Vestjens 1989, 1990; Kavanagh and Lambert 1990; Watson 2001), and many bird species are known to nest in mistletoe clumps (North 1906; Beruldson 1980). Several studies have documented the influence of mistletoe on distribution patterns of birds and mammals, both for individual species (Thompson and Owen 1964; Watson 1997) and entire assemblages (Smith 1984; Turner 1991; Watson 1994;

Watson *et al.* 2000). All studies (both in Australia and elsewhere) of the influence of mistletoe on faunal diversity are based on correlative data, comparing areas with naturally varying mistletoe densities (Bennetts and Hawksworth 1992). Hence, it remains equivocal whether mistletoe has a direct causal impact on diversity patterns. Researchers have noted that other factors covary with mistletoe abundance, including soil fertility and the density of large herbivores (Dean *et al.* 1994), which may affect diversity patterns independently.

Removal experiments allow direct measurement of interaction strength, and permit the functional importance of individual ecosystem constituents to be quantified (Mills *et al.* 1993). Thus, the direct effect of mistletoes on community composition can be measured by comparing control sites with sites in which all mistletoe plants have been experimentally removed. A landscape-scale experiment of this nature presents many logistical challenges, and to date it has not been attempted. There have been several experimental removals to assess the effect of mistletoe infection on tree health (e.g. Minko and Fagg 1989; Reid *et al.* 1994), but the level of treatment was the individual tree, and so cannot address the ecosystem-level role of mistletoe abundance.

Here, I compare the avifauna of two adjacent woodland remnants, one of which had been cleared of mistletoe plants for the past four years by the landholder. Despite involving only two sites without replication, this allows the keystone hypothesis (Watson 2001) to be addressed explicitly for the first time. According to this hypothesis, plots in which

mistletoe plants have been removed are predicted to have, *inter alia*,

(1) lower abundances of mistletoe-obligate frugivores and folivores, with populations declining toward local extinction;

(2) lower abundances of regular mistletoe foragers (folivores, frugivores and nectarivores);

(3) lower abundances of birds and mammals that nest in mistletoe clumps and hollows; and

(4) lower richness of vertebrates generally

than control plots (Watson 2001).

Avian data presented here will be used to evaluate these predictions, explore factors to be considered when designing a landscape-scale experiment, and address the importance of mistletoe to woodland-dependant birds.

Study Area and Methods

This study was carried out in two adjacent woodland remnants near Gundaroo, in the southern tablelands of New South Wales close to the border with the Australian Capital Territory (35°02′S, 149°14′E, 620 m above sea level). The remnants are of comparable area (33 and 36 ha) separated by a narrow unsealed road. The vegetation in both remnants is open grassy woodland dominated by *Eucalyptus blakelyi*, *E. rossii* and *E. macrorhyncha* with occasional *E. polyanthemos* and *E. bridgesiana*. *E. mannifera* is common on ridges, with *E. melliodora* and occasional *E. largiflorens* growing near the edges. The understorey is dominated by native and introduced grasses with few shrubs. Both remnants have a single dam and several intermittent streams. Starting in 1996, the owner of one of these blocks has systematically killed mistletoe plants in the remnant using an oxygen–acetylene blowtorch and a trailer-mounted cherry-picker to reach higher clumps. This process has been repeated once a year since then, resulting in greatly reduced mistletoe abundance throughout the remnant (referred to hereafter as the treatment site). The landholder is concerned about biodiversity on her land — especially declining woodland birds — and has employed this management strategy in the belief that it will improve tree health and habitat quality. No mistletoes have been removed from the adjoining remnant (hereafter referred to as the control site) and densities are typical of remnant vegetation in the region. The land surrounding both remnants is open pasture dominated by introduced grasses. Historically, both remnants were under the same ownership and grazed by sheep and cattle. The treatment site was fenced off in 1996 and has since been ungrazed, whereas the control site has been accessible (and presumably grazed at low intensity) by several horses since 1987.

Both sites exhibited high homogeneity of vegetation, so mistletoe abundance and tree density were quantified by counting all individuals within a 50 × 50 m plot located in the centre of each remnant. Informal sampling of vegetation conducted while censusing birds confirmed that the plots were representative of the overall remnant in terms of tree density and mistletoe abundance (unpublished data). Phenology of both mistletoe plants and eucalypts was noted and percentage coverage of leaf litter, grass and bare ground was quantified using four 1-m^2 quadrats (located at the corners of the plot).

The assemblage of birds inhabiting both remnants was sampled in two separate inventories (spring, 5–8 September 2000, and summer, 5–7 January 2001) encompassing winter residents and summer migrants. In each inventory, 10 one-hour censuses were conducted in both remnants, with species recorded as either present or absent (species seen flying over the remnant were not included). These censuses ranged from immediately after dawn until dusk, alternating

between the two remnants to minimise confounding effects. During each census, I walked slowly throughout the remnant, using both vocalisations and visual cues to identify birds to species. Hence, for each species there are 20 one-hour samples for each remnant in which they were recorded as present or absent. This frequency measure is used as a surrogate of relative abundance, estimating site preference for each species. In addition to computing total species richness for each site and richness of woodland-dependent species (defined here as species that feed and nest primarily within woodland or forest), birds were classified as mistletoe nesters and/or mistletoe feeders on the basis of published information (Reid 1986; Barker and Vestjens 1989, 1990).

To assess whether the assemblages of species occurring in both sites were sampled to the same degree of completeness, species-accumulation curves were constructed from these data and richness of the sites predicted. By dividing observed richness by predicted richness, a percentage value of sample completeness similar to a confidence interval can be derived (Peterson and Slade 1998). To obtain a value for estimated richness (*S*) I used the Chao (1984) estimator equation:

$$S = S_{obs} + a^2 / 2b$$

where S_{obs} is the number of species observed during sampling, *a* is the number of species encountered in only one sampling period, and *b* is the number of species seen in two or more periods (after Peterson and Slade 1998). Note that these estimated richness values were calculated solely to evaluate sample completeness — actual species richness values were used for all tests.

Differences in the frequency of woodland birds, mistletoe feeders and mistletoe nesters were tested using one-tailed Wilcoxon signed-ranks tests, with species frequencies in the two remnants treated as paired observations (Rosner 1995).

Results

Tree density was similar in both sites, with 209 trees in the 50 × 50 m plot in the control site and 212 in the treatment site. Percentage cover of leaf litter, bare ground and grass were quantified, and showed no significant differences between sites (Table 1), although litter depth appeared greater in the control site. Mistletoe density differed greatly, with 23 plants in the control plot and 2 in the treatment plot (Table 1), a difference reinforced by informal observations throughout the remnants during censusing. Most mistletoe plants were *Amyema pendulum*, but several *Amyema miquelii* were recorded parasitising large *E. largiflorens* in the control

Table 1. Summary of attributes and vegetation characteristics of the remnants

'Treatment' denotes the woodland remnant in which mistletoe plants were regularly killed, whereas 'Control' denotes the adjoining patch where mistletoe density had not been manipulated

Variable	Treatment	Control
Area (ha)	36	33
Maximum elevation (m)	664	642
Richness of canopy trees	8	8
Tree density (in 0.25-ha plot)	212	209
Mistletoe density (in 0.25-ha plot)	2	23
% cover leaf litter (mean ± s.d.)	72.5 ± 22.2	67.5 ± 33.0
% cover bare ground (mean ± s.d.)	22.5 ± 20.6	40.0 ± 40.6
% cover grass (mean ± s.d.)	11.25 ± 6.3	6.25 ± 9.5

Table 2. Species recorded in the two woodland remnants

Woodland richness is the number of woodland-dependant species observed in each inventory (those species not listed below as [A]). Estimated woodland richnesses were derived using the Chao estimator, explained in the text. Sample completeness was calculated by dividing estimated woodland richness by the observed woodland richness for each inventory, with 100% being the maximum value (estimated richness = observed richness)

Linnean Name	Common Name	Treatment		Control	
		Spring	Summer	Spring	Summer
Coturnix pectoralis[A]	Stubble Quail	–	–	–	4
Chenonetta jubata[A]	Wood Duck	7	2	3	3
Anas superciliosa[A]	Pacific Black Duck	1	–	2	–
Anas gracilis[A]	Grey Teal	1	–	–	1
Phalacrocorax melanoleucos[A]	Little Pied Cormorant	–	1	–	1
Egretta novaehollandiae[AC]	White-faced Heron	–	–	–	1
Aquila audax[A]	Wedge-tailed Eagle	2	–	–	–
Falco berigora[AC]	Brown Falcon	–	–	1	–
Falco longipennis[A]	Australian Hobby	2	–	1	–
Turnix varia	Painted Button-quail	–	2	–	–
Columba livia[A]	Feral Pigeon	1	–	–	–
Phaps chalcoptera[C]	Common Bronzewing	–	2	2	3
Ocyphaps lophotes[AC]	Crested Pigeon	3	1	–	3
Callocephalon fimbriatum[B]	Gang-gang Cockatoo	1	–	5	–
Cacatua roseicapilla[AB]	Galah	7	4	6	1
Cacatua galerita[A]	Sulfur-crested Cockatoo	9	9	6	7
Polytelis swainsonii[B]	Superb Parrot	–	8	2	10
Platycercus elegans[B]	Crimson Rosella	7	10	10	7
Platycercus eximius[B]	Eastern Rosella	8	9	8	9
Psephotus haematonotus	Red-rumped parrot	–	3	–	6
Cuculus pallidus[B]	Pallid Cuckoo	–	–	8	–
Cacomantis flabelliformis	Fan-tailed Cuckoo	–	–	3	–
Chrysococcyx lucidus	Shining Bronze-cuckoo	–	1	–	1
Dacelo novaeguineae	Laughing Kookaburra	4	9	8	7
Todiramphus sanctus	Sacred Kingfisher	–	4	–	–
Eurystomus orientalis[A]	Dollarbird	–	3	–	–
Cormobates leucophaeus	White-throated Treecreeper	10	10	10	10
Climacteris picumnus	Brown Treecreeper	–	–	–	1
Malurus cyaneus	Superb Fairy-wren	–	–	2	1
Pardalotus punctatus	Spotted Pardalote	7	4	10	3
Pardalotus striatus	Striated Pardalote	9	9	6	10
Sericornis frontalis	White-browed Scrubwren	1	–	–	–
Gerygone fusca	Western Gerygone	–	–	–	2
Gerygone olivacea	White-throated Gerygone	–	10	–	7
Acanthiza pusilla	Brown Thornbill	5	1	8	6
Acanthiza reguloides	Buff-rumped Thornbill	9	10	10	9
Acanthiza chrysorrhoa[C]	Yellow-rumped Thornbill	2	1	2	2
Acanthiza lineata	Striated Thornbill	10	4	9	9
Acanthiza nana	Yellow Thornbill	–	–	–	3
Smicrornis brevirostris	Weebill	–	–	3	3
Anthochaera carunculata[BC]	Red Wattlebird	–	–	3	–
Philemon corniculatus[BC]	Noisy Friarbird	–	10	–	8
Manorina melanocephala[BC]	Noisy Miner	5	9	10	10
Lichenostomus penicillatus[BC]	White-plumed Honeyeater	–	–	2	3
Melithreptus brevirostris[B]	Brown-headed Honeyeater	2	–	1	3
Microeca fascinans	Jacky Winter	3	–	4	3
Petroica phoenicea	Flame Robin	5	–	–	–
Petroica multicolor	Scarlet Robin	1	–	–	–
Petroica rosea	Rose Robin	–	–	2	–
Eopsaltria australis	Eastern Yellow Robin	2	3	3	2
Daphoenositta chrysoptera	Varied Sitella	1	7	5	4
Falcunculus frontatus	Crested Shrike-tit	1	–	–	–
Pachycephala pectoralis	Golden Whistler	1	–	–	–

Table 2.   Continued

Linnean Name	Common Name	Treatment		Control	
		Spring	Summer	Spring	Summer
Pachycephala rufiventris[C]	Rufous Whistler	–	10	–	8
Colluricincla harmonica[C]	Grey Shrike-thrush	5	7	7	3
Myiagra rubecula	Leaden Flycatcher	–	10	–	9
Rhipidura leucophrys[C]	Willy Wagtail	–	–	3	2
Rhipidura fuliginosa	Grey Fantail	10	10	10	10
Coracina novaehollandiae[B]	Black-faced Cuckoo-shrike	3	7	–	6
Oriolus sagittatus[B]	Olive-backed Oriole	–	–	–	3
Cracticus torquatus[C]	Grey Butcherbird	–	–	–	1
Grallina cyanoleuca	Magpie-lark	3	5	7	10
Gymnorhina tibicen[C]	Australian Magpie	10	10	10	10
Strepera graculina[BC]	Pied Currawong	4	–	4	–
Corvus coronoides[B]	Australian Raven	9	2	8	4
Corcorax melanorhamphos	White-winged Chough	–	–	10	–
Alauda arvensis[A]	Common Skylark	3	1	5	3
Hirundo neoxena[A]	Welcome Swallow	–	–	4	–
Hirundo nigricans[A]	Tree Martin	–	1	4	–
Zosterops lateralis[B]	Silvereye	–	–	–	2
Sturnus vulgaris[A]	Common Starling	2	–	5	–
Total richness per inventory		39	37	43	48
Woodland richness		28	29	33	39
Estimated woodland richness		28.5	29.2	33.0	39.1
Sample completeness		98.1	99.4	99.9	99.7

[A]Open-country species, waterbirds, aerial foragers, raptors and exotic species.
[B]Species reported to feed on mistletoe (derived primarily from Reid 1986; Barker and Vestjens 1989, 1990).
[C]Species known to nest in mistletoe clumps (see, for example, North 1906; Beruldson 1980).

site. *A. pendulum* was observed with flower buds in spring, and had abundant flowers and several unripe fruits. *A. miquelii* plants had some flower buds in summer, but no fruit. No eucalypts were flowering in spring, but *E. mannifera* and *E. macrorhyncha* had abundant flowers in summer.

In total, 71 bird species were recorded from within the two remnants; of these, 52 were recorded in the treatment site and 61 in the control site (Table 2). No mistletoe-obligate species were recorded, but a pair of Olive-backed Orioles, a species known to be an occasional disperser of mistletoe (Liddy 1982), was observed in the control site. In terms of woodland-dependent species (excluding waterbirds, raptors, aerial foragers, open-country and exotic species), 53 species were recorded — 46 from the control site and 38 from the
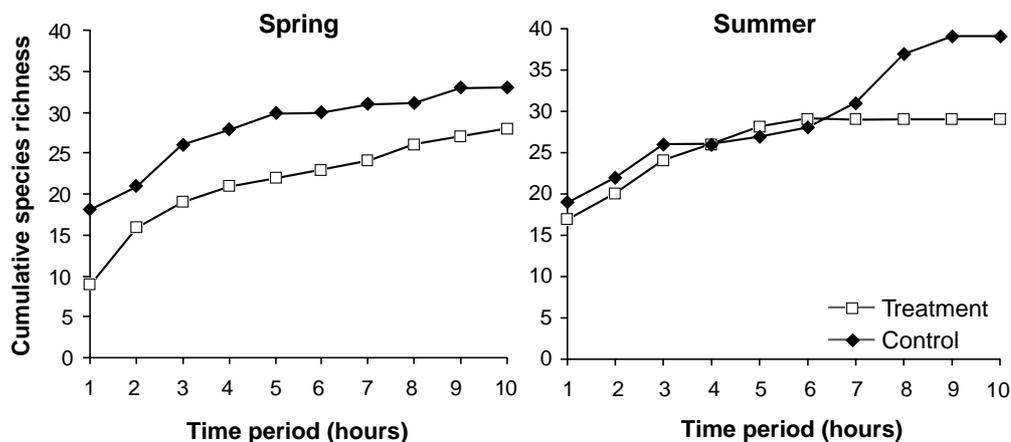

Fig. 1.   Species-accumulation curves for woodland-dependent species for the four inventories conducted in the two remnants, depicting the rate of addition of previously unencountered species. Each time period is a one-hour census, with each species recorded as either present or absent.

treatment site (Table 2). Estimated richness for both sites matched observed richness closely, with less than one additional species added to all four inventories. Sample completeness therefore exceeded 98% for all inventories, exceeding 99% for summer inventories when more woodland species were present. Thus, sampling of woodland species was relatively complete (Table 2; Fig. 1), enabling meaningful comparisons between sites. Of the 44 woodland species that differed in frequency of occurrence, 14 were more commonly recorded in the treatment site whereas 30 were more commonly recorded in the control site. The difference was found to be highly significant ($T = -235$, $n = 44$, $P << 0.005$ adjusted for ties). Of 15 woodland species recorded only in the control site, 13 (2 frugivores, 2 nectarivores, 9 insectivores) were recorded more than once. Of 7 woodland species found only in the treatment site, 3 (1 generalist and 2 insectivores) were recorded more than once (Table 2).

Of the 16 species known to feed on mistletoe (flowers, fruit and nectar), 13 occurred at different frequencies in the two sites: 3 species were more commonly recorded in the treatment site and 10 were more commonly recorded in the control site. The difference was significant ($T = -18$, $n = 13$, $P \approx 0.0287$ adjusted for ties).

Of the 15 species known to nest in mistletoe clumps, 4 were more frequently recorded in the treatment site, 2 occurred equally frequently in both sites and 9 were more frequently recorded in the control site; the difference was not statistically significant ($T = -24$, $n = 13$, $P > 0.05$).

Discussion

The two woodland remnants I examined are of comparable area and similar in all vegetation characteristics measured except mistletoe density, which was artificially manipulated. They have similar grazing histories, support the same set of microhabitats and are separated only by a narrow unsealed road. Variance in avian community composition can thus be related primarily to the 10-fold difference in mistletoe abundance, allowing the first direct evaluation of the role of mistletoe in affecting diversity.

The control site was more diverse than the treatment site, in terms of both total richness (9 more species, 17.3%) and for woodland-dependant species (8 more species, 21.1%). However, this comparison is based on limited data, so rather than dwell on differences in species presence/absence, it is more meaningful to examine the relative frequency of occurrence of species, effectively indicating site preferences at a finer resolution. Of 44 woodland species that occurred at different frequencies in the two sites, almost 70% were more frequently recorded in the control patch, and those species known to forage on mistletoe showed a stronger, highly significant pattern. These are important findings, and demonstrate that mistletoe density can indeed function as a determinant of avian diversity, reinforcing previous correlative studies (Rice *et al.* 1981; Bennetts 1991; Bennetts *et al.* 1996).

Interestingly, this pattern was not restricted to nectarivores and frugivores, extending to many insectivorous species. Species recorded only in the control patch included foliage gleaners (Yellow Thornbill, Weebill), ground foragers (White-winged Chough), snatchers and pouncers (Pallid Cuckoo, Fan-tailed Cuckoo, Rose Robin, Grey Butcherbird), salliers (Willy Wagtail) and scansorial gleaners (Brown Treecreeper). Indeed, I regularly observed several species foraging (particularly Brown Thornbill, also Grey Shrike Thrush, Rufous Whistler) and perching (Buff-rumped Thornbill, Leaden Flycatcher, Striated Thornbill, Grey Fantail) in mistletoe clumps.

The far-reaching effects of mistletoe density on a range of avian guilds have been noted by others. Bennetts (1991), working in coniferous forests in the Rocky Mountains, noted that all feeding guilds but one had a positive response to mistletoe density — stands with more mistletoes had higher richnesses and abundances of birds (Bennetts 1991; Bennetts *et al.* 1996). The only exception was nectarivores — unlike most Australian mistletoes, Palearctic dwarf mistletoes (Viscaceae, *Arceuthobium*) are insect- and wind-pollinated. In eucalypt-dominated forest near Eden, New South Wales, Turner (1991) noted higher foraging activities in areas with more mistletoe plants, suggesting that mistletoe was one of the key factors influencing avian distribution patterns within the region. Finally, research in Buloke woodlands in western Victoria (Watson 1994, 1997; Watson *et al.* 2000) revealed a positive association between richness of woodland birds and both mistletoe density and richness.

Interestingly, no obligate mistletoe frugivores were recorded in either woodland remnant. The Mistletoebird (*Dicaeum hirundinaceum*) is regarded as an uncommon migrant to the southern tablelands (Wilson 1999), and is presumably the main agent of mistletoe dispersal in this landscape. The only other mistletoe fruit specialists likely to be found — Spiney-cheeked Honeyeater (*Acanthogenys rufogularis*), Striped Honeyeater (*Plectorhyncha lanceolata*) and Painted Honeyeater (*Grantiella picta*) — are considered either rarities or vagrants in the southern tablelands (Wilson 1999). Olive-backed Orioles were observed and are known to disseminate mistletoe seeds occasionally but are not regarded as mistletoe specialists (Reid 1991). Many insects are mistletoe specialists, including butterflies, moths, flies, thrips, psyllids and true bugs (de Baar 1985). Two mistletoe specialist lepidopterans (*Comocris behri*, Noctuidae; *Delias aganippe*, Pieridae) were observed only in the control patch and, although these groups were not specifically sampled in this study, this finding does support the prediction that specialists decline in areas without mistletoe.

Richness and frequency of mistletoe-nesting species were both higher in the control plot, but there was no significant difference between the remnants. Of the 15 species known to

use mistletoe clumps as nest sites, only 4 (Noisy Friarbird, Red Wattlebird, Yellow-rumped Thornbill and Grey Butcher-bird) commonly use them (North 1906; Ford 1999); the latter three of these were more common in the control site. Whether an absence of mistletoe entails fewer available nest sites cannot be addressed sufficiently, and must await a larger-scale investigation.

In terms of the predictions presented earlier, there is general support. Predictions 2 and 4 were both strongly supported — the site with less mistletoe had significantly lower frequencies of birds known to feed on mistletoe, and substantially lower richness of birds generally. Prediction 1 was (serendipitously) supported, with two mistletoe-specialist folivores (lepidopterans) recorded only in the control site. Prediction 3 was not supported, there being no significant difference between the sites in terms of frequency of species known to nest in mistletoe.

Mistletoe density in the two remnants differed dramatically — approximately 8 plants per hectare in the treatment site, and 92 per hectare in the control site (extrapolated from the 0.25-ha sample). Turner (1991) recorded densities of 7–10 mistletoes per hectare in continuous eucalypt forest near Eden, with similar values reported from other undisturbed habitat (Smith 1984). Thus, using continuous undisturbed forest as the reference, the control plot in this comparison might be more accurately termed an augmented site, containing approximately ten times the normal number of mistletoe plants. Note, however, that this is an unrealistic comparison given the highly fragmented nature of this habitat, with few large continuous tracts remaining. Rather than being anomalous, this remnant is representative of most woodland remnants throughout the region, most of which support similar densities of mistletoe (unpublished data). Indeed, other fragmented habitats in Australia are known to have superabundant mistletoes (Heather and Griffin 1978; Norton et al. 1995; Norton and Reid 1997) and this pattern may be a more general response of eucalypt forests to fragmentation.

To guide future experimental approaches to understanding the effects of mistletoe on diversity, several factors should be considered. Adequate replication is essential to enable the effects of mistletoe to be quantified accurately, with treatment assigned randomly to minimise confounding effects of other variables. Based on the findings reported here, the distance between sites need not be great. While there may be greater differences between sites further apart, even adjacent sites can exhibit dramatic differences in faunal composition. Efforts should be made to ensure that removal sites are absolutely free of mistletoe plants, with follow-up removals necessary at least annually. Cross-taxon approaches are recommended, especially the inclusion of folivorous insect groups. Finally, some additional habitat measures are recommended, notably litter depth and number of hollows and fallen branches.

The management implications of this case-study are important, given the widespread view of mistletoe as a noxious weed in Australian woodlands. Rather than having a deleterious effect on biodiversity, as is popularly held, mistletoe density had a direct positive effect on species richness. A difference of over 20% of woodland-dependent species is considerable, especially given the declining status of many of these species. The Brown Treecreeper, a species that has undergone dramatic declines throughout its range, was recorded only in the control patch. Similarly, the endangered Superb Parrot, a species known to feed on mistletoe nectar and flowers (Webster 1998), was more frequently recorded in the control plot (in flocks of up to 40 individuals). So, in examining distribution patterns of these and other declining woodland species, and in formulating management responses to ensure their survival, attention should be given to mistletoe as a key factor.

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