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# Fragmentation, Disturbance, and Plant Distribution: Mistletoes in Woodland Remnants in the Western Australian Wheatbelt

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**Abstract:** *Spatial heterogeneity and patchy distributions of species in intact landscapes are likely to lead to complex and unpredictable distribution patterns in remnants following fragmentation. We examined this proposition in relation to the mistletoe *Amyema miquelii*, which exhibits a clumped distribution in *Eucalyptus salmonophloia* woodlands in the Western Australian wheatbelt. We sampled mistletoe distribution and abundance in 14 woodland fragments ranging from 2.4 to 60.5 ha and in 14 sections of roadside corridors. These sites represent all known fragments and corridors containing *E. salmonophloia* in a 1680-km<sup>2</sup> study area. We found that large fragments were more likely to have mistletoes than small fragments, but that small fragments either contained many or few to no mistletoes, reflecting the way fragmentation "samples" the pre-existing distribution. Superimposed on this sampling effect is the influence of disturbance. Fragments subjected to stock grazing contained no mistletoes. This indicates that grazing modified the habitat either for the mistletoe itself, through changed water relations, or for the frugivorous birds which may disperse mistletoe fruit, through removal of the shrubby understory. Only one *A. miquelii* plant was found on 26.3 km of roadside corridor, despite tree densities in corridors being similar to those in fragments. Roadside areas are generally considered good habitat for mistletoes, and their absence suggested that fruit-dispersing birds either did not use the corridors or did not stay in them long enough to deposit mistletoe seeds. These results indicate that, in order to predict biotic responses to fragmentation, information on distribution patterns and scales of patchiness in the prefragmentation landscape is required and the effects of fragmentation per se are likely to be confounded by other factors such as disturbance. Furthermore, quantifying fragmentation effects is difficult because of the small sample sizes typical of highly fragmented landscapes.*

La fragmentación, perturbación y distribución de las plantas: los muérdagos en remanentes del bosque en el cinturón triguero de Australia occidental

**Resumen:** *La heterogeneidad espacial y la distribución en parches de especies en paisajes intactos son proclives a conducir a patrones de distribución complejos e impredecibles en los remanentes que suceden a la fragmentación. Examinamos este tema en relación al muérdago *Amyema miquelii*, una especie que exhibe una distribución contagiosa en los bosques de *Eucalyptus salmonophloia* del cinturón de trigo de Australia occidental. Muestreamos la distribución y abundancia del muérdago, en 14 fragmentos de bosques que oscilaban entre 2.4 y 60.5 ha y en 14 secciones de corredores de los bordes de rutas. Estos sitios representan todos los fragmentos y corredores conocidos que contienen *E. salmonophloia* en los 1680 km<sup>2</sup> del área de estudio. Encontramos que los fragmentos más grandes eran más proclives a tener muérdago que los fragmentos más chicos, pero los fragmentos más pequeños contenían mucho, poco o ningún muérdago, reflejando el modo en que la fragmentación "muestra" la distribución pre-existente. Superpuesto a este efecto de muestreo está la influencia de las perturbaciones. Los fragmentos sujetos a pastoreo de ganado no tuvieron muérdagos. Esta*

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Paper submitted December 6, 1993; revised manuscript accepted May 25, 1994.

*situación indica que el pastoreo modificó el hábitat para los muérdagos, a través del cambio en las relaciones bióticas, o bien para los pájaros frugívoros que pueden dispersar los frutos del muérdago, a través de la remoción de las áreas arbustivas del sotobosque. Sólomente una planta de *A. miquellii* fue encontrada en los 26.3 km de corredor a lo largo de la ruta, a pesar que la densidad de árboles en los corredores fue similar a la encontrada en los fragmentos. Las áreas a lo largo de las rutas son generalmente consideradas como buenos hábitats para los muérdagos, pero su ausencia sugiere que los pájaros dispersores de los frutos no utilizaron los corredores o bien no estuvieron un tiempo suficiente como para depositar las semillas de muérdago. Estos resultados indican que, a efecto de predecir las respuestas bióticas de la fragmentación, se requiere información sobre los patrones de distribución y las escalas de la distribución contagiosa del paisaje previo a la fragmentación. Los resultados también indican que los efectos de la fragmentación en sí mismos tienden a confundirse con otros factores tales como la perturbación. Más aún, la cuantificación de los efectos de la fragmentación resulta difícil debido al pequeño tamaño de muestra típico en los paisajes altamente fragmentados.*

## Introduction

Fragmentation strongly influences ecosystem components and processes. Several studies have documented the effect of habitat loss and isolation of remnant areas on the fauna in these fragments, with most showing a decline in species number (see Kitchener et al. 1980; Soulé et al. 1988; Saunders 1989; Robinson et al. 1992; Thomas et al. 1992). Fewer studies have shown similar changes for flora (Robinson et al. 1992), probably because of the more sessile nature and often longer lifespans of plants. Fragmentation also has a pronounced effect on biotic interactions and ecosystem processes, including water, nutrient, and energy cycling within remnant ecosystems (see Bond & Slingsby 1984; Saunders et al. 1991; Bierregaard et al. 1992; Hobbs 1993a). In addition, isolation increases the vulnerability of fragments to a variety of external influences, including biological invasions, grazing, timber harvesting, and hunting (Norton 1992; Scougall et al. 1993; Hobbs 1993a).

The long-term viability of a fragment is strongly influenced by its location within the broader landscape, and in particular by the nature of surrounding vegetation and land-uses and the presence of corridors. For example, many birds require a range of different vegetation types to survive, and their ability to persist in one vegetation type (where they may be important seed dispersers) is likely to depend on their ability to utilize other vegetation types (for example, for food or shelter: Saunders & Ingram 1987; Lambeck 1992). Both the nature of the intervening vegetation (natural or artificial) and the presence of movement corridors (Hobbs 1992) are likely to be important.

Landscape heterogeneity and the patchy distribution of many organisms are likely to add complexity to the effects of fragmentation. Fragmentation essentially results in the retention of a sample of the original landscape. The effects of heterogeneity and differing types of species distributions have been considered in detail for

quadrat sampling of vegetation, and it is clear that sampling efficiency varies greatly depending on types of distribution and size of sampling units (see Kershaw & Looney 1985). With small sampling units in particular, organisms with clumped or contagious distributions will occur either abundantly or not at all within sample quadrats. In a similar way, a process of fragmentation that leaves small remnant patches is likely to capture only a few examples of contagiously distributed species. Clearly, increasing the fragment size will increase the probability that such species are captured, simply as a result of the standard species-area relationship. When the effects of fragmentation on both individual species and communities are studied, however, the scale of patterning of both landscapes and organisms must be considered. While the question of scale in landscape ecology is receiving increasing attention (see Urban et al. 1987; Kotliar & Weins 1990; Allen & Hoekstra 1991), it has only recently been discussed in relation to fragmentation (Lord & Norton 1990; Angelstam 1992; Harris & Silva-Lopez 1992). The patterns and scales of the original landscape patches and of the organisms contained in them form the backdrop to the subsequent effects of fragmentation, which superimposes a further set of patterns and scales (sizes, distributions, and connectivity of remnants).

Fragmentation is also a nonrandom process; in the Western Australian wheatbelt, for instance, woodland soils were better for agriculture and hence were cleared first and most extensively. The remainder is therefore not a representative sample of what was there originally. The superimposition of fragmentation on an already complex landscape is likely to produce further complexity that may be currently inexplicable without reference to the original landscape. If no examples of the unfragmented landscape exist, it could be impossible to understand the effects of fragmentation.

Hemiparasitic mistletoes from the family Loranthaceae are good examples of species that have a natu-

rally patchy distribution. Loranthaceae mistletoes are a distinctive feature of the Australian flora, with approximately 72 species. Australian mistletoes are distributed contagiously across the landscape, and their presence depends on both biotic factors—bird dispersal patterns (Reid & Lange 1988; Reid & Yan in press), and physical factors—soil water and nutrient status (D. Norton & M. Stafford Smith, unpublished data). The distribution and abundance of mistletoes in fragments likely depends on both their spatial arrangement before fragmentation (some fragments will lack mistletoes because none were present prior to fragmentation) and on the impact of fragmentation on the birds involved in pollination and dispersal. Mistletoes are almost totally dependent on birds for dispersal to suitable germination sites (Liddy 1983; Reid 1989, 1990, 1991).

We looked at the distribution and abundance of the mistletoe *Amyema miquelii* (nomenclature follows Green [1985] and Brooker and Kleinig [1990] for *Eucalyptus*) in woodlands dominated by *Eucalyptus salmonophloia* (salmon gum), and we interpreted our findings in the context of fragmentation. A number of predictions can be made about the likely effects of fragmentation on mistletoes; we used these as the framework for this study. These predictions are as follows:

- (1) Mistletoes are likely to occur more often in larger fragments than in smaller fragments.
- (2) If the distribution of mistletoes is naturally contagious, mistletoe abundance in small fragments is likely to be bimodally distributed, with some fragments having none and some having abundant mistletoes because of sampling effects.
- (3) Disturbed fragments are likely to have fewer mistletoes than undisturbed fragments because disturbance such as livestock grazing is likely to degrade the woodland habitat and hence reduce the establishment and survival of mistletoes.
- (4) Mistletoe density in corridors is likely to be similar to that in fragments if corridors act either as habitat for mistletoes or if they are important movement routes for mistletoe-dispersing birds.

## Methods

The study was undertaken north of Kellerberrin in the central Western Australian wheatbelt (31° 23' S, 117° 45' E). This area has been the subject of an extensive research program on the effects of fragmentation on remnants of native vegetation (Saunders et al. 1993). This 1680-km<sup>2</sup> study area was the focus of our investigation. Like the rest of the wheatbelt, the Kellerberrin area has been extensively cleared over the past 100

years, with only 7% of the original vegetation remaining, primarily as small fragments (<100 ha). The study area has a Mediterranean-type climate with an annual rainfall of about 350 mm that falls mostly in winter. Summer maximum temperatures can exceed 40°C, and winter minimums can drop below 0°C. The landscape is one of limited relief, and a typical catenary sequence can extend for several kilometers, with deep sands and laterites on the uplands, duplex soils on the slopes, and heavier soils and salt-lake systems in the valleys.

Before clearing for agriculture, the vegetation was a mosaic of woodland and shrubland communities, broadly related to soil type (McArthur 1993). *Eucalyptus salmonophloia* woodlands occurred predominantly on heavier soils in valley floors and were disproportionately affected by land clearance, with very few remnants remaining. These woodlands are characterized by an open canopy of *E. salmonophloia* (up to 20 m tall), either in pure stands or mixed with *E. salubris*, *E. capillosa*, and *E. loxophleba*. Multi-stemmed *Eucalyptus* species (mallee) may also be present. A well-developed shrub stratum up to 1–2 meters tall is present and is composed of species such as *Acacia hemiteles*, *Scaevola spinescens*, *Olearia muelleri*, and *Atriplex* spp. In the presence of grazing by domestic livestock, the shrub stratum is severely depleted, and nonnative herbaceous species may invade.

We endeavored to sample all fragments and roadside corridors within the 1680-km<sup>2</sup> study area containing abundant *Eucalyptus salmonophloia*, including grazed and ungrazed areas. Field work was undertaken during March–May 1993. Within each fragment, 10-meter-wide transects were located 50–100 meters apart. To avoid possible edge effects, transects were located at least 50 meters in from fragment edges. Along each transect the species, height, and diameter at breast height (1.3 m) of all trees was recorded, and the species and number of mistletoe clumps were noted. Host tree ages were not determined because of a poor association between growth ring number and tree age in *E. salmonophloia*, although in intact woodland stem diameter and age have been shown to be correlated (Department of Conservation and Land Management, unpublished report). We aimed to sample 5–10% of the area of each *E. salmonophloia* fragment with our transects. *E. salmonophloia* fragments were inbedded in either remnants containing other vegetation types (e.g., shrubland) or in agricultural fields and were isolated from other woodland fragments.

Corridor sampling was based on roadside corridors containing at least 1 km of relatively continuous *Eucalyptus salmonophloia*. Areas lacking *E. salmonophloia* were not sampled. The species, diameter, and height of all trees were recorded, and the species and abundance of any mistletoes noted. Corridor width was measured

as the distance from the road edge to the limit of the corridor. Where the roadside corridor was present on both sides of the road, only one side was sampled. Because of the mosaic nature of the original vegetation, *E. salmonophloia* corridors are not always contiguous with *E. salmonophloia* fragments and are often separated by other vegetation types such as shrubland.

## Results

Fourteen *Eucalyptus salmonophloia* fragments ranging in size from 2.4 to 60.5 ha were identified in the study area (Table 1), within which we sampled 6.3% of the total *E. salmonophloia* area. Some *E. salmonophloia* fragments were totally surrounded by other native vegetation such as shrubland (sites 3 and 4 in Durokoppin Nature Reserve, Table 1), but more commonly they were isolated from other native vegetation by agricul-

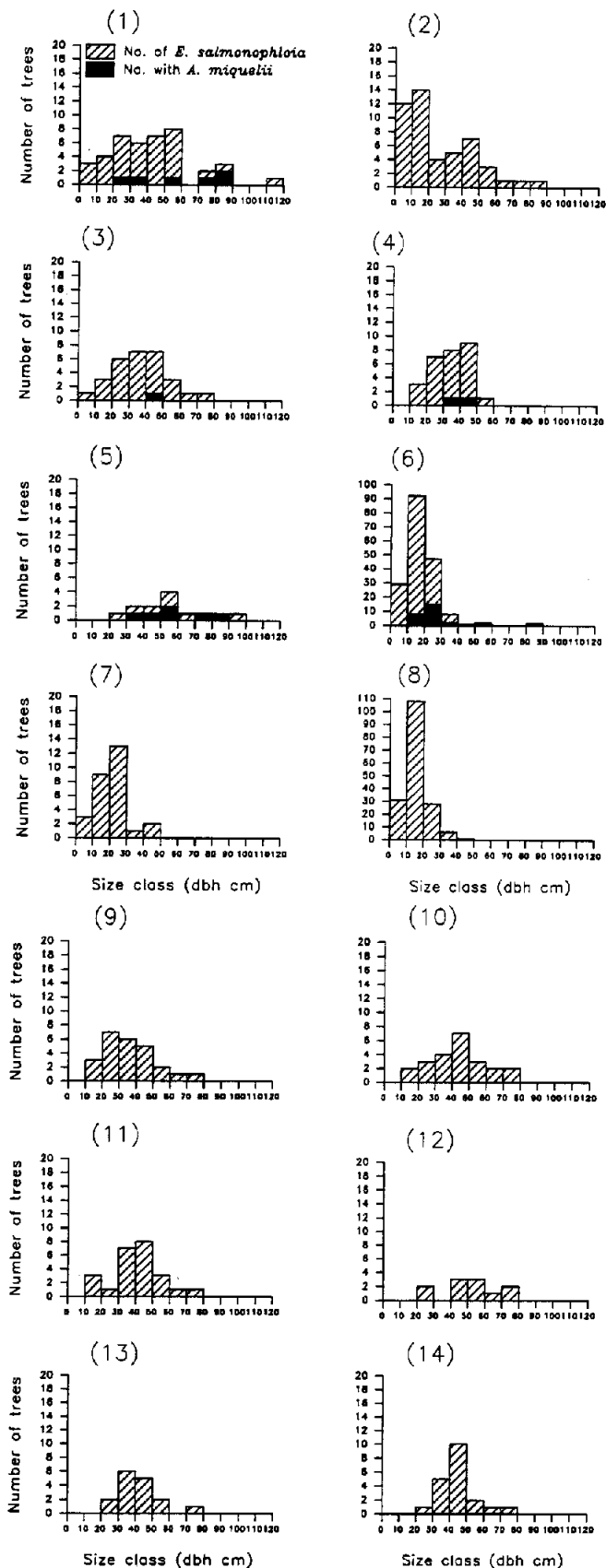
tural land to varying degrees, with some completely isolated (for example, sites 11, 12, and 13, Table 1, [Riley's, Nock's and York's]). Six of the fragments have been subjected to continual sheep grazing since fragmentation (about 50 years), and the remaining eight fragments have been virtually free of sheep grazing over this period.

Size-class distributions of *Eucalyptus salmonophloia* were discontinuous, with most trees occupying a narrow range of diameters (Fig. 1) and by implication a narrow range of ages. Individual sites varied, however, ranging from those dominated by relatively large-diameter trees (for example, site 5 [Moore's E] and site 12 [Nock's]) to those dominated by relatively small-diameter trees (for example, site 6, North Baandee and site 8, Kununoppin; (Fig. 1)). *E. salmonophloia* density is generally inversely related to tree size, with sites like Moore's E and Nock's having low densities (29.5 and

Table 1. Characteristics of woodland fragments in the Western Australian wheatbelt.

Characteristic	1	2	3	4	5	6		
Total Fragment Area (ha)	113.0	40.0	1030.0	1030.0	~150.0	199.0		
<i>E. salmonophloia</i> Area (ha)	~47.0	~12.0	~23.0	~2.5	~2.4	~20.4		
Ungrazed/Grazed	U	U	U	U	U	U		
Transect Area (ha)	3.97	1.2	1.2	0.47	0.44	1.55		
Total Number of Trees	202	195	205	95	49	251		
Total Density (trees/ha)	50.9	162.5	170.8	202.1	111.4	161.9		
Number <i>E. salmonophloia</i>	41	48	29	28	13	181		
<i>E. salmonophloia</i> Density (trees/ha)	10.3	40.0	24.2	59.6	29.5	116.8		
Number (%) Trees with Live <i>A. miquelii</i>	12 (5.9)	2 (1.0)	2 (1.0)	2 (2.1)	5 (10.2)	27 (10.8)		
Number (%) Trees with Dead <i>A. miquelii</i>	1 (0.5)	2 (1.0)	0	0	4 (8.2)	4 (1.6)		
Number (%) Trees with Live and Dead <i>A. miquelii</i>	13 (6.4)	4 (2.1)	2 (1.0)	2 (2.1)	9 (18.4)	31 (12.4)		
Mean Number Live <i>A. miquelii</i> /Infected Tree	2.2 ± 2.12	2.0 ± 1.41	1.5 ± 0.71	1.5 ± 0.71	2.6 ± 2.07	1.5 ± 0.84		
Mean Number Live and Dead <i>A. miquelii</i> /Infected Tree	2.3 ± 2.72	1.8 ± 0.96	2.5 ± 0.71	1.5 ± 0.71	5.0 ± 5.43	1.5 ± 0.85		
Characteristic	7	8	9	10	11	12	13	14
Total Fragment Area (ha)	~81.0	~60.5	~4.0	~20.0	~4.5	~6.5	~5.5	~4.3
<i>E. salmonophloia</i> Area (ha)	~4.5	~60.5	~4.0	~12.9	~4.5	~6.5	~5.5	~4.3
Ungrazed/Grazed	U	U	G	G	G	G	G	G
Transect Area (ha)	0.5	1.02	0.43	0.85	0.48	0.36	0.4	0.41
Total Number of Trees	325	201	46	57	41	34	54	50
Total Density (trees/ha)	650.0	197.1	107.0	67.1	85.4	94.4	135.0	122.0
Number <i>E. salmonophloia</i>	28	174	25	23	24	11	16	21
<i>E. salmonophloia</i> Density (trees/ha)	56.0	170.6	58.1	27.1	50.0	30.6	40.0	51.2
Number (%) Trees with Live <i>A. miquelii</i>	0	0	0	0	0	0	0	0
Number (%) Trees with Dead <i>A. miquelii</i>	0	0	0	0	0	0	0	0
Number (%) Trees with Live and Dead <i>A. miquelii</i>	0	0	0	0	0	0	0	0
Mean Number Live <i>A. miquelii</i> /Infected Tree	0	0	0	0	0	0	0	0
Mean Number Live and Dead <i>A. miquelii</i> /Infected Tree	0	0	0	0	0	0	0	0

<sup>a</sup> (1) Minniberri Water Reserve; (2) Huandanning Water Reserve; (3) Durokoppin Nature Reserve, southeast corner; (4) Durokoppin Nature Reserve, center; (5) Moore's East; (6) North Baandee Nature Reserve; (7) Higginson; (8) Kununoppin township site; (9) Moore's West; (10) Gents; (11), Riley's; (12) Nock's; (13) York's; (14) Leake's.



**Figure 1.** Diameter-class frequency distributions for *Eucalyptus salmonophloia* at the eight ungrazed (1–8) and six grazed fragments (9–14). See Table 1 footnote for site names.

30.6 trees per ha) and North Baandee and Kununoppin high tree densities (116.8 and 120.6 trees per ha; Table 1), suggesting that *E. salmonophloia* trees become established after large-scale disturbance. This is certainly the case for North Baandee, Kununoppin, and Higginson (site 7), which became established after fire, land clearance, and timber extraction, respectively. A cohort of young trees was also present at Huandaning (site 2; Fig. 1), where a localized fire had occurred.

We also sampled 14 roadside corridors 1.1–3.5 km long (Table 2) that varied in width from 3 to 22 meters and were always adjacent to agricultural land. The corridors all had healthy *Eucalyptus salmonophloia* overstory, although often only one tree wide, but the understory varied from a well-developed shrub stratum to a largely naturalized herbaceous ground cover. Some corridors were linked to fragments with *E. salmonophloia* (for example, Baandee North Rd), but most were isolated, either because the road edge contained other natural vegetation types (such as shrubland or mallee) or because it terminated (such as at a road junction).

Total tree density (all *Eucalyptus* species) and that of *E. salmonophloia* did not differ significantly between the fragments and roadside corridors based on single-factor analyses of variance ( $F = 0.090$ ,  $p = 0.766$ , and  $F = 0.011$ ,  $p = 0.918$ , respectively). There was considerable variation between individual sites, however, with means and standard deviations for total tree densities of  $165.5 \pm 150.8$  trees per ha in the fragments and  $146.9 \pm 110.8$  trees per ha in the roadside corridors. Means and standard deviations for *E. salmonophloia* densities were  $54.6 \pm 56.2$  trees per ha and  $41.8 \pm 44.0$  trees per ha for fragments and roadside corridors respectively.

The mistletoe *Amyema miquelii* was recorded along transects in six of the 14 fragments and was also present in one further fragment (site 7, Higginson) that was not part of our transects. No other mistletoe species were observed. A *miquelii* was recorded on 61 of the 1805 trees measured in the fragments (3.4%), although this varied from 18.4% of trees in Moore's E (site 5) to no trees in several other fragments (Table 1). On some trees, particularly at the Moore's E site, only dead *A. miquelii* were present. Because we may have failed to record some trees with very small *A. miquelii* plants, all analyses were based on both live and dead *A. miquelii* as an overall index of mistletoe infestation. For those trees with *A. miquelii*, the number of plants present on individual host trees ranged from 1 to 17, with fragment means of 1.5–5.0. A single-factor analysis of variance showed significant differences between sites ( $F = 2.508$ ,  $p = 0.041$ ), and the Moore's E site had a particularly high level of infestation ( $5.0 \pm 5.43$  mistletoes per host; Table 1).

Of the 61 trees with *Amyema miquelii*, 44 were *Eucalyptus salmonophloia* (72.1%). *A. miquelii* were

**Table 2. Roadside corridor characteristics in the Western Australian wheatbelt.**

Characteristic	Site Code <sup>a</sup>													
	A	B	C	D	E	F	G	H	I	J	K	L	M	N
Length (km)	2.2	1.6	2.1	1.5	1.3	2.5	3.5	1.9	1.1	1.9	2.1	1.7	1.5	2.4
Width (m)	4	22	22	22	22	2	22	22	22	22	10	2	3	2
Total Corridor Area (ha)	0.88	3.5	4.6	3.3	2.86	0.5	7.7	4.18	2.42	4.18	2.1	0.34	0.45	0.48
Total Number of Trees	75	314	267	156	214	146	857	272	229	415	478	109	70	187
Total Density (trees/ha)	85.2	89.7	58.0	47.3	74.8	292.0	111.3	65.1	94.6	99.3	227.6	320.6	155.6	389.6
Number <i>E. salmonophloia</i>	41	24	125	95	157	60	351	123	62	123	89	39	25	77
Density (trees/ha)	46.6	6.9	27.2	28.8	54.9	120.0	45.6	29.4	25.6	29.4	42.4	114.7	55.6	160.4
Number (%) of Trees with Live <i>A. miquelii</i>	0	0	0	0	0	1 (0.7)	0	0	0	0	0	0	0	0

<sup>a</sup> (A) Gents Road; (B) Minniberrri Road 1; (C) Minniberrri Road 2; (D) Purdy Road 1; (E) Purdy Road 2; (F) Ryans Road; (G) Baandee North Road; (H) Doodlakine-Kununoppin Road 1; (I) Doodlakine-Kununoppin Road 2; (J) Doodlakine-Kununoppin Road 3; (K) Kellerberrin-Trayning Road; (L) Yorkrakine Road; (M) Morley Road; (N) Bungulla-Yelbeni Road.

also present on *E. loxophleba* (4 trees, 6.6%), *E. capilliosa* (3 trees, 4.9%), *E. salubris* (5 trees, 8.2%), and three mallee species (5 trees, 8.2%) (Table 3). Based on a Pearson goodness-of-fit test, the observed proportion of trees infested with *A. miquelii* was significantly different from their proportional abundance in the fragment woodlands ( $X^2 = 34.69$ , 4 df,  $p < 0.001$ ). *A. miquelii* was more common on *E. salmonophloia* than expected, less common on *E. salubris*, *E. capilliosa*, and the mallee *Eucalyptus* species, and in proportion with its hosts abundance on *E. loxophleba*.

*Amyema miquelii* occurred on *Eucalyptus salmonophloia* trees from 20 to 100 cm diameter, and no clear relationship occurred between size class and the degree of infestation (Fig. 1). There was a significant correlation, however, between the number of *A. miquelii* plants per *E. salmonophloia* tree and tree diameter ( $r = 0.601$ ,  $n = 44$ ,  $p < 0.001$ ), and larger trees tended to have more individuals of *A. miquelii*.

There was a strong positive association between frag-

ment size and the presence of mistletoes, with mistletoes present in three of the four fragments of more than 20 ha (75%), one of the two fragments of 10–19.9 ha (50%), and two of the eight fragments of less than 10 ha (25%). There was a weak negative association, however, between fragment size and proportion of infected trees (Fig. 2a), with the highest proportion of infected trees in the smallest fragment (site 5, Moore's E). There was no obvious association between fragment size and the mean number of *Amyema miquelii* plants per infected host tree (Fig. 2b), although the site with the highest number of *A. miquelii* plants was the smallest (Moore's E). In both the large fragments with *A. miquelii* (site 1, Minniberrri, and site 2, North Baandee), *A. miquelii* appeared to be contagiously distributed (Fig. 3), although the fragments were not large enough to quantify adequately the scale at which this occurred.

Six of the 14 fragments had been grazed, and none of these had *Amyema miquelii* (Table 1). *A. miquelii* were recorded in transects in six of the eight ungrazed

**Table 3. Number of *Eucalyptus* trees by species in each fragment and number of trees with live and dead *Amyema miquelii* in parentheses.**

Species	Site Code <sup>a</sup>													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>E. salmonophloia</i>	41 (8)	48 (0)	29 (1)	28 (2)	13 (6)	181 (27)	28 (0)	174 (0)	25 (0)	23 (0)	24 (0)	11 (0)	16 (0)	21 (0)
<i>E. salubris</i>	77 (1)	40 (0)	—	—	—	53 (4)	—	10 (0)	—	18 (0)	14 (0)	10 (0)	10 (0)	1 (0)
<i>E. loxophleba</i>	42 (1)	73 (3)	2 (0)	—	—	—	—	—	—	4 (0)	—	—	7 (0)	—
<i>E. capilliosa</i>	—	—	96 (1)	57 (0)	9 (2)	—	197 (0)	—	17 (0)	—	—	—	—	10 (0)
Mallee <i>Eucalyptus</i> spp. <sup>b</sup>	40 (3)	34 (1)	78 (0)	10 (0)	27 (1)	17 (0)	100 (0)	17 (0)	4 (0)	12 (0)	3 (0)	13 (0)	21 (0)	18 (0)

<sup>a</sup> (1) Minniberrri Water Reserve; (2) Huandanning Water Reserve; (3) Durokoppin Nature Reserve, southeast corner; (4) Durokoppin Nature Reserve, center; (5) Moore's East; (6) North Baandee Nature Reserve; (7) Higginton; (8) Kununoppin township site; (9) Moore's West; (10) Gents; (11) Riley's; (12) Nock's; (13) York's; (14) Leake's.

<sup>b</sup> The mallee *Eucalyptus* species are *E. celastroides*, *E. eremophila*, *E. erythronema*, *E. hypochlamydea*, *E. myriadena*, *E. sheathiana*, *E. subangusta*, *E. transcontinentalis* and *E. yilgarnensis*.

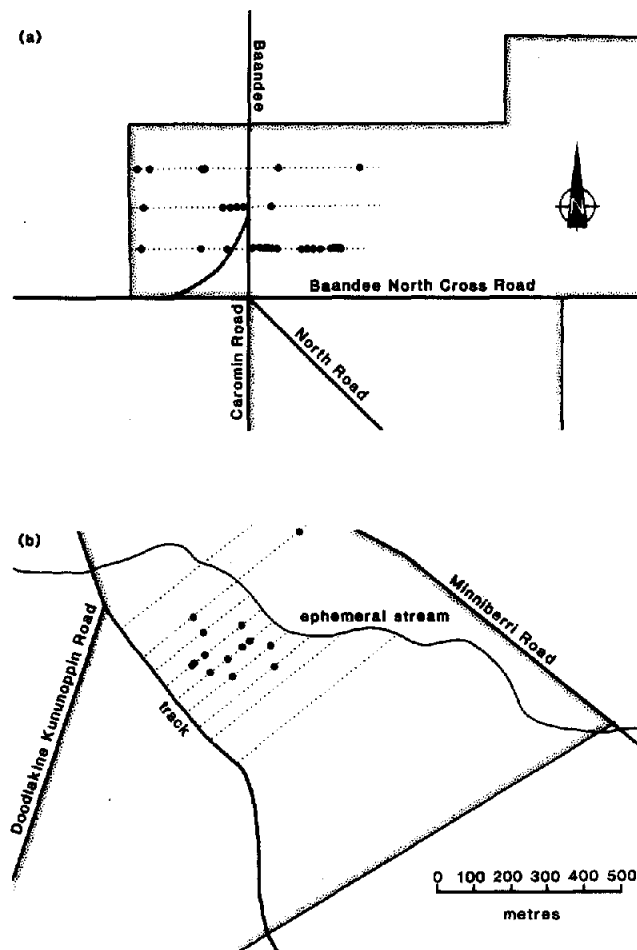


Figure 2. Spatial distribution of sampled trees with (●) and without (○) *Amyema miquelii* along sample transects in the (a) North Baandee site 6 and (b) Minniberry, site 1, fragments.

fragments and in the additional fragment where *A. miquelii* was observed, which was also an ungrazed site. There was a significant negative association between grazing and the presence of *A. miquelii* ( $X^2 = 7.875$ , 1 df,  $p = 0.001$ ). The adjacent grazed and ungrazed Moore's E site (site 5) and Moore's W site (site 9) clearly showed this marked difference in infestation.

Only one *Amyema miquelii* plant was recorded along 26.3 km of roadside corridor, and it was present on *Eucalyptus yilgarnensis*. This represents significantly fewer plants than expected based on mistletoe abundance in the fragments (goodness-of-fit test,  $X^2 = 132.7$ , 1 df,  $p < 0.001$ ). The corridors surveyed represented virtually all corridors within the study area dominated by *E. salmonophloia*.

## Discussion

Two difficulties with analyzing and interpreting the data collected here were the small number of sites available

for analysis and the small number of mistletoes encountered. This limits the power of statistical tests, but it is a genuine feature of this highly fragmented landscape and highlights a major problem in understanding the consequences of fragmentation. We tried to sample all fragments and corridors containing *Eucalyptus salmonophloia* within the study area, and we believe that our data provide a realistic picture of mistletoe distribution in the area. We suspect that the sample-size problems we have encountered are not unique to Western Australia and are probably common in other studies aimed at understanding the consequences of fragmentation.

*Amyema miquelii* is a widespread Australian mistletoe that mainly parasitizes *Eucalyptus* species but can be locally common on *Acacia* species (Barlow 1984). Although it appears able to parasitize a range of *Eucalyptus* species across Australia, *A. miquelii* is usually fairly host-specific at a particular site. In eastern Australia, for example, Reid and Yan (in press) found it preferentially parasitizing a subset of the available *Eucalyptus* species (*E. blakelyi*, *E. dealbata*, *E. melliodora*, *E. albens*, *E. bridgesiana*). In central Australia it is commonly found on some mallee *Eucalyptus* species and *E. camaldulensis* but does not parasitize other common species including *E. papuana* and *E. terminalis* (D. Norton, personal observation). In the forests of southwestern Australia, Keneally (1973) observed *A. miquelii* parasitizing *E. wandoo* and *E. calophylla* but not the common *E. marginata*. Lamont (1985) observed that *A. miquelii* parasitized 54% of *E. calophylla* and 1% of *E. marginata* at a site near Perth, but it did not parasitize nine other *Eucalyptus* species present at the site. The preferential parasitism of *E. salmonophloia* in our study (Table 3) is therefore typical of the more general infestation pattern of *A. miquelii*.

As a framework for assessing the effects of fragmentation on the distribution of the mistletoe *Amyema miquelii* in *Eucalyptus salmonophloia* woodland remnants in the Western Australian wheatbelt, we evaluated the four propositions previously outlined based on our results.

(1) *Mistletoes occur more often in larger than in smaller fragments.* Our data show clearly that mistletoes were more often present in large fragments than in small fragments. Few studies have shown clear evidence that changes in plant-species abundance depend on fragment size, although Robinson et al. (1992) found that clonal plants were particularly sensitive to fragmentation, being much less likely to persist in small fragments than nonclonal plants. Mistletoes appear to respond to habitat reduction in a similar manner to other organisms, with a loss of individuals and populations from small fragments. Mistletoes are likely to be particularly sensitive to fragment area effects because both the mistletoe plants and their avian dispersers are affected by habitat reduction—through edge effects or stochastic



tion of dead mistletoes at Moore's E (71%) suggests that this may be starting to happen at this site.

(3) *Disturbed fragments are likely to have fewer mistletoes than undisturbed fragments.* Our results showed a strong negative association between fragment disturbance (grazing) and mistletoe presence, such that mistletoes were absent from all grazed fragments (Fig. 1). The association is clear, but the reasons for it are complex and likely to involve factors affecting the quality of the habitat both for pollinating and dispersing birds and for the mistletoe itself.

The wheatbelt avifauna has changed substantially with land clearance. Some species have become locally extinct and many others are far less common than they were previously (Saunders & Curry 1990; Saunders 1993). The Mistletoe Bird (*Dicaeum hirundinaceum*) is the predominant disperser of mistletoe fruit in Australia (Liddy 1983), but other birds, including honeyeaters, may be important (Reid & Yan in press). Mistletoe Birds are probably extinct within the study area (D. A. Saunders, personal communication), and this may be the single most important factor determining the current distribution of mistletoes. Other species that are potential dispersers of mistletoe fruit include the Singing, Brownheaded, and Spiny-cheeked Honeyeaters (*Lichenostomus virescens*, *Meliphreptus brevirostris*, and *Acanthorhynchus superciliosus*), the Red Wattlebird (*Anthochaera carunculata*), and the Yellow-throated Miner (*Manorina flavigula*). These species have all declined in the wheatbelt (Saunders 1993), and the Red Wattlebird and Spiny-cheeked Honeyeater are both uncommon in the Kellerberrin area (D. A. Saunders, personal communication). The other species, while still relatively common (Cale 1990; Lynch & Saunders 1991), all differ markedly from the Mistletoe Bird in their movement and foraging patterns. All are generalist foragers that move extensively about the landscape, and none are known definitely to feed on mistletoe fruit. We observed Singing Honeyeaters feeding alternatively on *Amyema miquelii* in tree canopies and shrubs in the understorey. The distribution of Singing Honeyeaters is known to depend particularly on the presence of an intact shrub stratum (Cale 1990). The loss of this stratum could thus indirectly influence the dispersal of mistletoe fruit. Shrub cover and density was significantly lower in a grazed *Eucalyptus salmonophloia* fragment than in an ungrazed fragment in the study area (R. Hobbs & D. Norton, unpublished data). Not enough is known, however, about the role of extant bird species in fruit dispersal to allow us to further assess their hypothesis.

Grazing also appears to alter the habitat of the mistletoe itself by altering water relations within the *Eucalyptus salmonophloia* woodlands. Mistletoes are both water and nutrient parasites (Ehleringer et al. 1985) and are totally dependent on their host for these. Several

studies with Australian mistletoes have shown that they consistently have higher rates of water use than their host (Ullmann et al. 1985; Davidson et al. 1989), with host-to-mistletoe transpiration ratios of 1.5–7.9. In arid central Australia, mistletoes are more abundant along road edges, where they occur on host plants with higher relative water contents than plants of the same host species away from the road edge (D. Norton & M. Stafford Smith, unpublished data). Mistletoes are therefore likely to be sensitive to reductions in water availability to host trees.

In a separate study we have shown that grazed *Eucalyptus salmonophloia* woodlands are characterized by significantly higher soil temperatures, lower litter cover, and more compacted soils than ungrazed woodlands (R. Hobbs & D. Norton, unpublished data). Increased soil compaction and reduced litter is likely to reduce infiltration of water into the soil (McFarlane et al. 1993), and increased soil temperatures will increase evaporation and reduce water available to the host and mistletoe. Other work in *E. salmonophloia* woodlands has shown that the reproductive success of *E. salmonophloia* is decreased in grazed woodlands (C. Yates personal comm.). Scougall et al. (1993) found fewer trees and greater amounts of dead wood in grazed *Acacia acuminata*–*E. loxophleba* woodlands. Grazing also facilitates the invasion of nonnative annual grasses (Scougall et al. 1993), which may compete with the shallow-rooted *E. salmonophloia* for soil water. Although no physiological data is available, these observations suggest that grazing reduces water availability to woody vegetation. It would seem reasonable to expect, given the greater water demand of mistletoes, that this will in turn affect the suitability of trees in grazed woodlands as sites for mistletoe establishment and growth.

It would therefore seem likely that grazing affects *Amyema miquelii* distribution both by altering the habitat for mistletoe-dispersing birds and by modifying woodland water relations, although our data do not allow us to assess the relative importance of these two factors. But both of these reduce the suitability of grazed woodland fragments for the establishment and growth of *A. miquelii* and probably play a major role in the total absence of this species from the grazed fragments we studied.

(4) *Mistletoe density in corridors is likely to be similar to that in fragments if corridors act either as habitat for mistletoes or if they are important movement routes for mistletoe dispersing birds.*

Our data showed almost total absence of *Amyema miquelii* from corridors dominated by *Eucalyptus salmonophloia* in the study area (Table 2), despite a search of 27.3 km of corridor. This occurred whether the corridor was contiguous with a *E. salmonophloia* fragment or not. *E. salmonophloia* corridors may pro-

vide habitat for mistletoes in their own right (acting as linear fragments), or they may be important routes for mistletoe-dispersing birds moving between fragments. The absence of mistletoes could therefore be due to corridors providing unsuitable habitat for mistletoes, mistletoe-dispersing birds not using the corridors, or dispersing birds not using the corridors in ways that sustain mistletoe populations.

Although corridors are open sites, other studies suggest that they are good habitat for mistletoes. For example, Lamont and Southall (1982) found that elsewhere in Western Australia there were over 10 times more *Amyema preissii* per potential host tree (*Acacia acuminata*) along a road verge than in an adjacent nature reserve, and Keneally (1973) observed more *A. miquelii* on roadside trees than in intact forest. In eastern Australia, a predominance of mistletoes on roadside trees has also been observed (Reid & Yan in press), and in central Australia, dense aggregations of mistletoes are common at roadside sites. Increased nutrient and water availability (Cale & Hobbs 1991; van Schagen et al. 1992; D. Norton & M. Stafford Smith, unpublished data), fewer perching sites per unit area, and increased movement of birds along the corridors (Lamont & Southall 1982) may be responsible for the increased abundance in other areas. In several of these studies, corridors appear to be good mistletoe habitat whether they are contiguous with fragments or not. It would therefore seem that physical aspects of habitat quality do not explain the absence of mistletoe in our study areas.

Several studies have investigated the value of roadside corridors for avifauna in the wheatbelt (Cale 1990; Lynch & Saunders 1991; Saunders & de Rebeira 1991), and their results are in general agreement. While roadside corridors are well used by birds, the composition of the avifauna is different from that in intact woodlands. Several invasive species are dominant in corridors, but many of the woodland interior birds are only rarely present. Avifaunal composition is strongly influenced by vegetation type, and particularly by the presence of a shrub layer. Cale (1990) found that Brownheaded Honeyeaters were absent from corridors lacking a shrub stratum, and Singing Honeyeaters were significantly less abundant. Birds that may disperse mistletoes may pass through corridors dominated by *Eucalyptus salmonophloia*, but it seems that without a well-developed shrub layer they are unlikely to reside and hence are unlikely to sustain mistletoe populations.

Our data suggest that *Eucalyptus salmonophloia* corridors up to the width we studied (22 m) are of little value as mistletoe habitat. This happens despite birds using these corridors, probably because *E. salmonophloia* corridors lack a shrub stratum as habitat for resident birds. *Amyema miquelii* is totally dependent on birds for dispersal, either within corridors or from

fragments into corridors, and will not persist in their absence. Thus corridors represent fundamentally very different and possibly unavailable habitat from the perspective of *A. miquelii*.

## Conclusions

Organisms with patchy distributions in natural landscapes, such as mistletoes, present particular problems for conservation. Because of sampling effects, there is a real chance that remnant fragments may not contain the organism of interest. Recent developments in reserve design that seek to maximize biodiversity in reserve networks (Margules et al. 1988; Margules & Stein 1989) need to take into account patchy distributions. This problem appears to be particularly bad in the Western Australian wheatbelt, where the natural landscape was historically patchy, but similar problems are likely to occur elsewhere. In our example, we have a naturally patchy landscape containing species that have patchy distributions within individual landscape units. Conservation biologists need to be aware that patchiness can occur at a range of scales in the landscape.

Our results show that, while a woodland structure may persist at a site, grazing appears to have major effects on other components of the system (such as birds), which in turn affect mistletoes and probably other species. Main (1992) suggested that the decline in the abundance of two butterfly species (*Ogyris* sp. Lycaenidae, *Deltis aganippe* Pieridae) in the Western Australian wheatbelt is due to declines in the abundance of mistletoes because the larvae of these butterflies feed on mistletoe foliage. While a woodland may appear structurally intact, the system may still be highly degraded because of the loss of other species and the loss or modification of important ecosystem processes (Norton 1992; Hobbs 1993a). Clearly the conservation value of grazed *E. salmonophloia* woodlands is considerably less than ungrazed ones.

A clear result of our study is the identification of strong interdependences between the effects of fragment size, sampling, and grazing on mistletoe distribution and abundance. The confounding influences of these factors are difficult to unravel because of the small sample sizes that occur in such highly fragmented landscapes (both in terms of numbers of fragments and numbers of mistletoes within fragments), but we sampled all fragments and corridors containing *Eucalyptus salmonophloia* present in our 1680-km<sup>2</sup> study area. Because of the effects of fragmentation in this type of landscape (and the Western Australian wheatbelt is by no means unique) and because of the confounding effects of fragment size, sampling, and grazing, we may have trouble ever fully understanding fragmented systems because

they are so small and so few. It is simply not possible in many cases to obtain further information in order to make more precise predictions on fragmentation effects.

Advocacy for the retention or provision of corridors in the landscape is predicated on the assumption that they will be of value in allowing movement of biota between isolated fragments. Recent debate has focused on the lack of evidence for this assumption and on possible negative aspects of corridors (Hobbs 1992; Simberloff et al. 1992). Our results suggest, as found in other studies (van Schagen et al. 1992), that corridors in the Western Australian wheatbelt exhibit dynamics markedly different from larger remnant areas. The fact that virtually no mistletoe was found in corridors suggests that fruit-dispersing birds either do not use the majority of corridors, do not spend long enough in them to deposit seeds, or do not move between remnants and road verges in time-scales relevant for mistletoe dispersal. While this does not preclude the possibility that the woodland corridors are used for movement, it certainly indicates that we should be careful in assessing their role, given that they will be expensive to manage and maintain.

The paucity of mistletoes in our study area contrasts sharply to their abundance in other agricultural areas, especially in eastern Australia where they are often regarded as pests (Reid & Yan in press). Two factors appear important. First, the preclearance landscape of the wheatbelt was characterized by a relatively fine mosaic of different plant communities. This would have imposed a strong patchy distribution on mistletoes in this landscape, which, together with the naturally contagious distribution of mistletoes, would have resulted in the large proportion of remnants lacking mistletoes. Second, the nature of land clearance in the wheatbelt appears different from that in eastern Australia or other areas of Western Australia where mistletoes are more common. Fragmentation in the wheatbelt left a landscape dominated by agricultural fields, with very few residual trees outside fragments and corridors. In contrast, the post-clearance landscape of much of eastern Australia has a far higher proportion of trees remaining (McIntyre & Barrett 1992). We believe that these differences in fragmentation have a profound influence on the fate of individual species remaining. In particular, the very course-grained landscape (see Lord & Norton 1990) of the wheatbelt appears to be far less conducive to species survival than the finer-grained landscape of eastern Australia. Clearly, fragmentation has different effects in different places, making it difficult to make generalized predictions about biotic responses.

In trying to tease out the causes of present-day mistletoe distribution in the highly fragmented landscape of the Western Australian wheatbelt, we differentiated between a diversity of spatial and temporal effects that

influence mistletoe distribution, including historical distribution, sampling effects, area effects, and the effects of post-fragmentation perturbations such as grazing. It is not easy to ascribe the observed patterns of mistletoes to a single factor such as fragment size, a situation that has also been observed for the New Zealand mistletoe *Trilepidea adamsii*, now presumed extinct (Norton 1991). Nor is it realistic to believe that a single factor is responsible for the decline of mistletoes; none of the factors we have discussed are mutually exclusive. It may be that in these highly fragmented landscapes we will never be able to fully understand the effects of fragmentation because the amount of change has already been so dramatic and because the effects of any one factor are confounded by other factors. While conservation biologists need to seek generalizable predictions about the effects of fragmentation, they cannot afford to gloss over the complexity of this task.

### Acknowledgments

We thank Carolyn McKenzie and V Saunders for assistance with field work, and Peter Cale, Andrew Hansen, Robert Lambeck, Nick Reid, Denis Saunders, and two anonymous referees for comments on the draft manuscript.

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