

**Box Mistletoe (*Amyema miquelii*)
occurrence and host condition in
Eucalyptus woodlands of the
Mount Lofty Ranges, South Australia**



Report for the Native Vegetation Council, South Australia

August 2004

Matthew Ward and David Paton

School of Earth and Environmental Sciences

University of Adelaide

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Front cover: Typical canopy dieback and mistletoe proliferation seen on Pink Gum *Eucalyptus fasciculosa* across the Mount Lofty Ranges, South Australia. This photo was taken in Sandy Creek Conservation Park.

1. Summary

In late 2003 grant money was awarded to the authors by the Native Vegetation Fund to undertake the first year of a three year project titled ‘Mistletoe dispersal by the Mistletoebird *Dicaeum hirundinaceum* in pink gum *Eucalyptus fasciculosa* woodlands of the Mount Lofty Ranges’. The first objective of this project was: ‘to document the relative abundance of mistletoe infestations in different eucalypt woodlands and develop a descriptive model of the habitat and host attributes which contribute to the prevalence (presence / absence) of mistletoe infestations’.

This objective was completed in 2004, and the following report focuses primarily on this part of the study. Much of this report follows closely the manuscript submitted for publication in June 2004 (attached to this report): *Ward, M.J. (under review).*

*Determinants of Box Mistletoe *Amyema miquelii* occurrence and host condition in Eucalyptus woodlands of the Mount Lofty Ranges, South Australia, Forest Ecology and Management.*

2. Key findings of study

- Pink gum *Eucalyptus fasciculosa* was the most common host of box mistletoe *Amyema miquelii*
- Woodland type was the primary influence of mistletoe prevalence (presence / absence) in eucalypt woodlands, more so than fragmentation, distance to an edge, soil type or topography
- The condition of pink gums in the Mount Lofty Ranges was very poor, with high levels of canopy dieback and epicormic growth
- The poor condition of pink gums is probably not due to box mistletoe abundance, as dieback levels are similar between host and non-host pink gums
- Taller pink gums with less canopy cover surrounding their own canopy are more likely to host box mistletoe
- Higher abundances of box mistletoe on pink gums compared with other Eucalypt types is probably an accumulative affect of:
 - Higher box mistletoe germination rates on pink gums than other Eucalypt types,
 - Higher than normal germination rates on stressed pink gums with canopy dieback compared to non-stressed pink gums with in-tact canopies; and
 - Large scale canopy dieback providing greater accessibility for Mistletoebirds to tree canopies and therefore more effective dispersal.

3. Introduction

3.1. Mistletoes

Mistletoes are flowering plants which parasitise the xylem sap of their host to obtain water and mineral nutrients, however, they provide their own photosynthetic products. The majority of Australian mistletoes are arboreal stem-epiparasites of the family Loranthaceae, represented by 12 genera and over 80 species (Barlow, 1992). Australian loranthaceous mistletoes are also characterised by having a close relationship with honeyeaters (Meliphagidae) for pollination, and on the Australian mainland the Mistletoebird *Dicaeum hirundinaceum* (Dicaeidae) is the most widespread disperser of mistletoe seeds (Schodde and Tidemann, 1986).

Many aspects of mistletoe biology have been studied throughout the world (Kuijt, 1969; Calder and Bernhardt, 1983). In Australia, research has considered mistletoe reproductive biology (Bernhardt, 1983), pollination and dispersal relationships (Keast, 1958; Liddy, 1983; Reid, 1989; Yan, 1993), seedling establishment (Yan and Reid, 1995) and the interrelationship between mistletoes, their hosts and the surrounding environment (Yan, 1990; Reid et al., 1992; Norton and Stafford Smith, 1999).

In the fragmented woodlands of south-eastern Australia, box mistletoe *Amyema miquelii* infects a wide range of eucalypt *Eucalyptus* species (Barlow, 1992; Downey, 1997). Since the early 1900s, there has been numerous reports of large increases in the abundance of mistletoe in these parts of rural Australia (Reid and Yan, 1995). It is generally accepted that these heavy infestations have occurred as a result of changes to a series of environmental filters which act to regulate mistletoe distribution and abundance. These primarily include: (1) improvements in environment habitat quality for mistletoes through fragmentation and suppression of tree regeneration; (2) lowering of herbivory pressures through declines in brush-tail possum (*Trichosurus vulpecular*) abundances; and (3) large scale suppression of canopy fires, from which mistletoes generally do not recover (Norton and Reid, 1997).

3.2. Tree decline and box mistletoe proliferation

Tree decline refers to the progressive decline in the health or numbers of trees in a landscape, and is a major conservation issue for temperate Eucalypt woodlands in Australia (Jameson, 1997). Symptoms of tree decline in individual trees can include

thinning of the tree crown, death of branches, an increase in epicormic shoot growth along the trunk or main branches and, if the tree has insufficient energy reserves to fight its maladies, eventual death of the entire tree (Heatwole and Lowman, 1986).

A variety of factors can contribute to tree dieback, including insect defoliation, fungal diseases such as *Phytophthora cinnamomi*, increased soil salinity, drought and soil nutrient imbalances (Heatwole and Lowman, 1986; Paton et al., 2000b; Reid and Landsberg, 2000). The consequences of tree decline include the decline of native biota, genetic loss, substrate loss, increased salinity, loss of aesthetic amenity and various socio-economic impacts (Heatwole and Lowman, 1986; Reid and Landsberg, 2000).

Mistletoe proliferation has also been implicated in tree decline in natural forests, plantations, orchards and ornamental trees around the world (Hawksworth, 1983). High mistletoe abundance may affect a host in a variety of ways, including reduction in height, diameter, foliage growth, and reproductive output, predisposition to attack by secondary agents such as insects and decay fungi, and premature mortality (Hawksworth, 1983).

In south-eastern Australia, tree decline, in particular in some *Eucalyptus* species, has also been attributed to apparent increases in mistletoe abundance, particularly box mistletoe *Amyema miquelii* (Ben Kahn, 1993; Yan and Reid, 1995; Norton and Reid, 1997). With reports of severe mistletoe infestations in rural Australia appearing frequently in the literature from about 1900 onwards (Heatwole and Lowman, 1986; Reid, 1997), concerned communities have repeatedly called for control of mistletoes because of the perceived threat to tree health (Reid et al., 1994).

The link between box mistletoe proliferations and rural tree decline, however, is not straightforward. High mistletoe abundances are symptomatic of broader landscape changes rather than the sole cause of tree decline (Reid et al., 1992), and the impact of mistletoe on eucalypt survival and growth can vary considerably between host species (Reid *et al.* (1994). Furthermore, there is an increasing awareness of the extreme importance of mistletoe to biodiversity (Watson, 2001; Watson, 2002), and the

widespread removal of mistletoe in response to a perceived threat to tree health could have significant impacts on local vertebrate and insect diversity.

Where mistletoe proliferations are perceived to occur, therefore, further research is required to determine the abundance of mistletoe, whether proliferations are having a negative impact on tree condition or mortality, and, if possible, the underlying drivers of proliferation.

3.3. *Box mistletoe in South Australia*

In South Australia, there is descriptive and anecdotal evidence of increases in the abundance of mistletoe and mistletoe proliferations. For example, a survey of mistletoe infestations in the Clare Valley, approximately 130 km north-east of Adelaide, found that box mistletoe affected approximately 40 % of available host species in the Valley, and approximately 34 %, 12 % and 19 % of the host trees in the valley were affected by slight, moderate and severe ‘infestations’ respectively (Ben Kahn 1993). This led to the development of a ‘Mistletoe Action Group’, which oversaw the removal of mistletoe from heavily infected eucalypts in the area. The group also raised community awareness of the broader issues relating to the management of mistletoe proliferations, including the benefits of mistletoe for biodiversity and the influence of habitat fragmentation on increased mistletoe abundance.

Yet mistletoe abundances in other woodlands in South Australia remain undocumented, despite certain taxa obviously carry higher mistletoe loads. In the Mount Lofty Ranges, for example, certain woodlands often carry heavy mistletoe loads and the condition of these trees is also often poor (authors’ observations). Quantitative data is therefore required to determine the relative abundance of box mistletoe on different host types, the associated effects on host tree condition, and to determine those factors which are driving mistletoe proliferations in the area.

The study described here investigates mistletoe abundances and tree health in temperate *Eucalyptus* woodlands of the Mount Lofty Ranges, South Australia. Specifically, the study objectives are to: 1) quantify the extent of mistletoe occurrence on different eucalypt types in the Mount Lofty Ranges; 2) investigate the relationship

between mistletoe prevalence with tree condition for the primary host of box mistletoe in the study area (pink gum *Eucalyptus fasciculosa*); and 3) examine how landscape features and individual tree characteristic influence box mistletoe prevalence (presence / absence) for a range of woodland types and for individual trees.

4. Methods

For a detailed description of the study methods and data analysis employed, see attached manuscript: *Ward, M.J. (under review). Determinants of Box Mistletoe Amyema miquelii occurrence and host condition in Eucalyptus woodlands of the Mount Lofty Ranges, South Australia, Forest Ecology and Management.*

4.1. Summary of study methods

- carried out in the southern Mount Lofty Ranges (MLR) of South Australia (138° 42' 28" E, 34° 58' 34" S), between July and November 2003
- confined to 30 National Parks and Conservation Parks of the MLR (Fig. 1)
- a three - tiered study, investigating box mistletoe occurrence at: 1) a landscape scale; 2) a woodland scale; and 3) an individual tree scale
- for landscape study, box mistletoe prevalence and landscape variables were assessed across 89 study sites, encompassing 4221 trees
- for pink gum woodland study, tree condition (canopy dieback and % epicormic growth) and box mistletoe prevalence was assessed for 1200 pink gums
- for individual tree study, architecture of individual trees and surrounding vegetation was assessed for 175 pink gums (95 host and 80 non-host)
- data analysis included descriptive statistics of mistletoe occurrence and tree condition
- data analysis also included logistic regression analysis of which habitat features influence mistletoe prevalence at a landscape scale, and how tree architecture influences mistletoe prevalence on individual pink gums

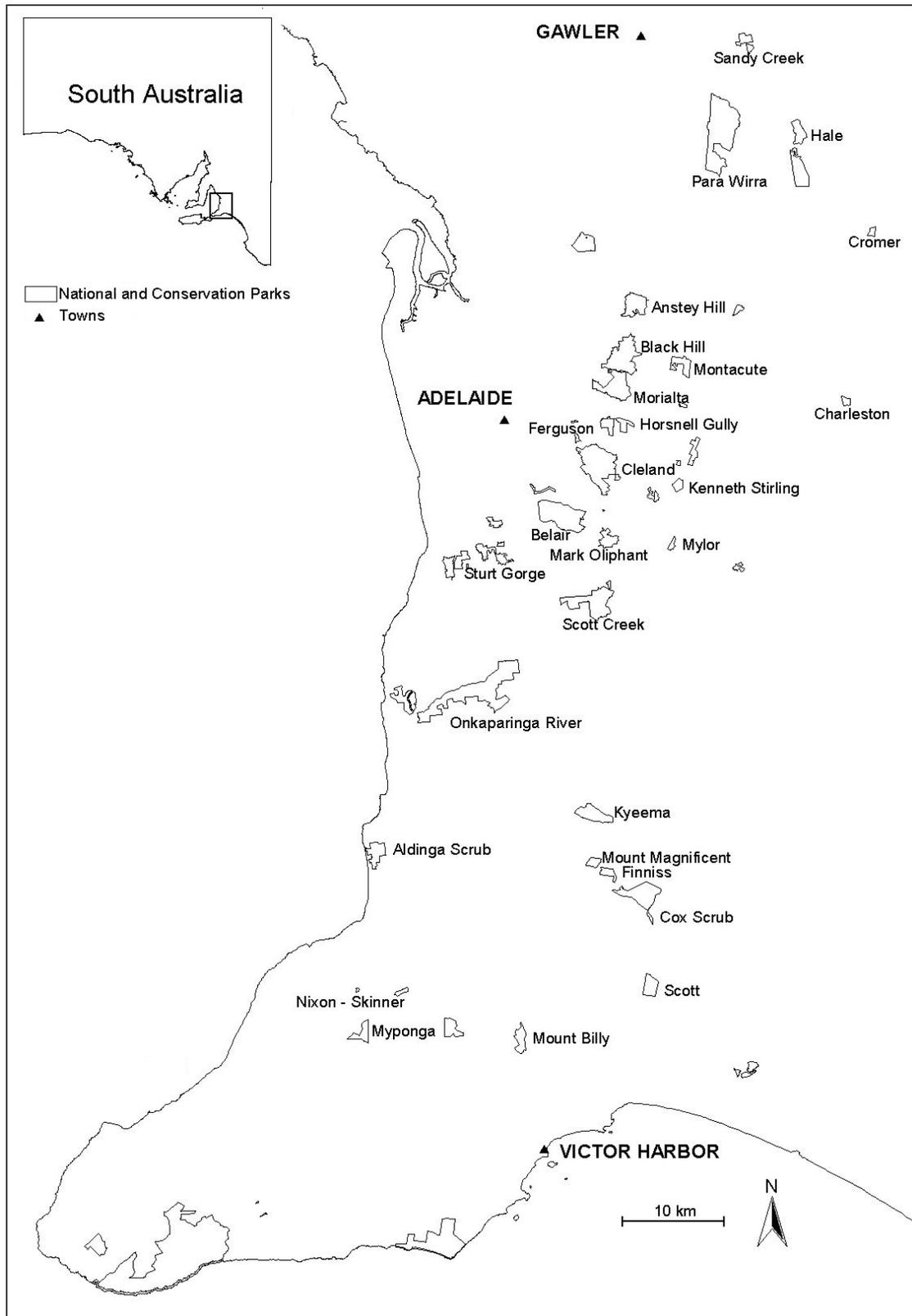


Figure 1. National and Conservation Parks in which the study was conducted. The individual tree – box mistletoe study was conducted in Sandy Creek, Cromer, Onkaparinga River and Aldinga Scrub Conservation Parks.

5. Results

For a detailed description of the study results, see attached manuscript: *Ward, M.J. (under review). Determinants of Box Mistletoe Amyema miquelii occurrence and host condition in Eucalyptus woodlands of the Mount Lofty Ranges, South Australia, Forest Ecology and Management.*

5.1. Summary of study results

Landscape features and box mistletoe prevalence (see Table 1)

- 13 % of all 4221 eucalypt trees hosted live box mistletoe
- 29 % of pink gums hosted live box mistletoe, followed by Blue Gum *E. leucoxyton* (11 %) and box eucalypts *E. microcarpa*, *E. odorata* and *E. porosa* (6%)
- 10 % of all pink gums had at least 3 live box mistletoe, compared with 3 % for blue gums and 1 % for box eucalypts
- logistic regression analyses demonstrated that mistletoe prevalence across the MLR was most influenced by woodland type, rather than by fragmentation, distance to the edge of vegetation, soil type or topography
- pink gum, blue gum and box eucalypt *woodlands* (as opposed to individual trees) had roughly equal probability of mistletoe being present

Pink gum woodland, tree condition and box mistletoe prevalence (see Table 2)

- for host pink gums, there was on average 2.8 live box mistletoe per tree, and 0.6 dead mistletoe per tree (see Plate 1)
- 44 % of pink gums hosted healthy box mistletoe, 39 % hosted healthy and unhealthy box mistletoe, and 17 % hosted primarily unhealthy mistletoe
- on average, canopy dieback on pink gums was 48 %
- 52 % of pink gums had at least 40 % ('substantial') canopy dieback (see Plates 2 and 3)
- on average, pink gums hosting box mistletoe had 58 % canopy dieback, non-host pink gums had 43 % canopy dieback
- on average, 39 % of the foliage of host and non-host pink gum canopies was made up of epicormic growth

Summary of study results (cont)

Individual tree features and box mistletoe prevalence (Table 3)

- compared to non-host pink gums, host pink gums were on average taller, had a larger girth, large canopy area and volume, were more planar in shape and had slightly greater levels of canopy dieback
- canopy cover surrounding host trees was less than for non-host trees, and host trees were generally taller relative to the surrounding vegetation
- the distance between host pink gums was smaller than between host and non-host trees, and there were more mistletoes within 5m of host pink gum canopies than for non-host canopies
- logistic regression analyses indicated that mistletoe prevalence on pink gums was primarily influenced by surrounding canopy cover and tree height

Table 1. Summary statistics of landscape features - box mistletoe *Amyema miquelii* study. n = the total number of each *Eucalyptus* species examined for box mistletoe. Three 'box' eucalypts (*E. microcarpa*, *E. odorata* and *E. porosa*) were combined because there were insufficient numbers for meaningful descriptive stats if considered individually. Table from: Ward, M.J. (under review) *Determinants of Box Mistletoe Amyema miquelii* occurrence and host condition in *Eucalyptus* woodlands of the Mount Lofty Ranges, South Australia, *Forest Ecology and Management*.

<i>Eucalyptus</i> species	n	% of trees hosting x live <i>A. miquelii</i>			# <i>A. miquelii</i> per host tree mean ± s.e. (n)
		x ≥ 1	x ≥ 3	x ≥ 5	
<i>E. fasciculosa</i>	1494	28.5	9.9	4.7	2.7 ± 0.1 (425)
<i>E. leucoxylon</i>	643	10.9	3.4	1.7	2.7 ± 0.4 (70)
<i>E. microcarpa</i> / <i>E. odorata</i> / <i>E. porosa</i>	228	5.3	1.3	0.9	2.3 ± 0.9 (13)
<i>E. cosmophylla</i>	163	4.3	0.6	0	N/A (7)
<i>E. camaldulensis</i>	465	2.2	0.7	0.2	2.9 ± 1.3 (10)
<i>E. viminalis</i>	232	0.4	0	0	N/A (1)
<i>E. baxteri</i> / <i>E. obliqua</i>	764	0.3	0	0	N/A (2)
<i>E. goniocalyx</i>	232	0.9	0	0	N/A (2)
Total (4221)	4221	12.6	4.2	2.0	2.7 ± 0.1 (530)

Table 2. Summary statistics of pink gum *Eucalyptus fasciculosa* woodland and box mistletoe *Amyema miquelii* survey. ‘Canopy dieback’ represents an estimation of the percentage of the potential canopy that is no longer present as a result of dieback. ‘Epicormic growth’ was estimated as that percentage of the present canopy that is made up of recent epicormic growth. A ‘host *E. fasciculosa*’ is classified as a Pink Gum with a live mistletoe on it. Table from: Ward, M.J. (under review) *Determinants of Box Mistletoe Amyema miquelii occurrence and host condition in Eucalyptus woodlands of the Mount Lofty Ranges, South Australia, Forest Ecology and Management*.

Measurement	Non – host	Host	All
	<i>E. fasciculosa</i> (n = 817)	<i>E. fasciculosa</i> (n = 383)	<i>E. fasciculosa</i> (n = 1200)
% of <i>E. fasciculosa</i> hosting live <i>Amyema miquelii</i>	-	-	31.9
% of <i>E. fasciculosa</i> hosting live or dead <i>A. miquelii</i>	-	-	37.8
# live <i>A. miquelii</i> per <i>E. fasciculosa</i> (mean ± s.e.)	-	2.8 ± 0.2	0.9 ± 0.1
# dead <i>A. miquelii</i> per <i>E. fasciculosa</i> (mean ± s.e.)	-	0.6 ± 0.1	0.2 ± 0.0
% <i>E. fasciculosa</i> with primarily healthy box mistletoe	-	44.3	
% <i>E. fasciculosa</i> with healthy and unhealthy box mistletoe	-	39.1	
% <i>E. fasciculosa</i> with primarily unhealthy box mistletoe	-	16.6	
% canopy dieback (mean ± s.e.)	43.3 ± 1.3	57.7 ± 1.7	47.9 ± 1.1
% epicormic growth (mean ± s.e.)	38.5 ± 1.5	39.4 ± 2.0	38.8 ± 1.2
% <i>E. fasciculosa</i> with at least 40 % canopy dieback	45.7	64.5	51.7

Table 5. Summary statistics of individual pink gum *Eucalyptus fasciculosa* / box mistletoe *Amyema miquelii* survey. ‘tree’ refers to *E. fasciculosa*, and ‘mistletoe’ refers to box mistletoe. ‘Host *E. fasciculosa*’ is a pink gum hosting a live box mistletoe. Table from: Ward, M.J. (under review). *Determinants of Box Mistletoe Amyema miquelii occurrence and host condition in Eucalyptus woodlands of the Mount Lofty Ranges, South Australia, Forest Ecology and Management*.

Measurement	Host <i>E. fasciculosa</i>	Non-host <i>E. fasciculosa</i>
	(mean ± s.e.)	(mean ± s.e.)
# trees surveyed (n)	95	80
Number of live mistletoe / tree	3.5 ± 0.4	N/A
Number of dead mistletoe	0.9 ± 0.2	N/A
Height (m)	6.8 ± 0.2	5.6 ± 0.2
DBH (Diameter at breast height, cm)	13.6 ± 0.6	10.3 ± 0.5
Canopy area (m ²)	29.9 ± 3.7	9.6 ± 1.6
Canopy volume (m ³)	93.1 ± 14.3	23.6 ± 5.3
CDR (Crown depth ratio)	0.5 ± 0.02	0.6 ± 0.02
CSR (Crown shape ratio)	1.5 ± 0.1	2.9 ± 0.4
% canopy dieback	48.3 ± 3.3	43.3 ± 4.1
Surrounding Canopy Cover (%)	21.7 ± 1.2	29.4 ± 1.1
Relative height difference between tree and surrounding vegetation (m)	+ 3.0 ± 0.2	+ 1.0 ± 0.2
Distance to nearest mistletoe infested tree (m)	7.0 ± 0.7	9.8 ± 1.3
Average # mistletoe within 5m of Pink Gum Canopy	4.2 ± 0.6	1.9 ± 0.3



Plate 1 Pink Gum *Eucalyptus fasciculosa* hosting probably at least 30 live box mistletoe *Amyema miquelii* in Anstey's Hill Conservation Park, South Australia.



Plate 2 Typical canopy dieback and mistletoe proliferation seen on Pink Gum *Eucalyptus fasciculosa* across the Mount Lofty Ranges, South Australia. This photo was taken in Sandy Creek Conservation Park.



Plate 3 A pink gum with a relatively in-tact canopy, and little or no mistletoes. This photo was taken in Aldinga Scrub Conservation Park, only 20 metres from numerous isolated trees with high mistletoe abundances.

6. Discussion

6.1. Landscape features and box mistletoe prevalence

Across the Southern Mount Lofty Ranges, the frequency and abundance of box mistletoe was considerably higher on *E. fasciculosa* than other eucalypt species. Although box mistletoe parasitises a wide range of Eucalypt hosts (Barlow, 1984; Downey, 1997), a relatively higher frequency and abundance on particular eucalypt types seen is not atypical (Lamont, 1985b; Reid et al., 1994; Yan and Reid, 1995; Downey et al., 1997; Fagg, 1997). The three most common hosts of box mistletoe in the MLR, *E. fasciculosa*, *E. leucoxylon* and three box eucalypts *E. porosa*, *E. microcarpa* and *E. odorata*, are all classified within the *Adnataria* section of the *Symphomyrtus* sub genus (Nicolle, 1997). This confirms Fagg's (1997) observations that *Symphomyrtus* Eucalypts are more susceptible to hosting mistletoe than are *Monocalyptus* Eucalypts such as Stringybarks (e.g. *E. baxteri* and *E. obliqua*).

The present study demonstrated that approximately 30 % of pink gums hosted mistletoe. Although this is lower than some of the aforementioned studies, comparison of the methodologies indicate mistletoe abundance on pink gums in the MLR is, in fact, particularly high. For example, the surveys of Reid and Yan (1995) and Lamont (1985b) focused on isolated farm trees and vegetation corridors, where mistletoe abundances are generally higher than in remnant vegetation. The present study, however, was conducted across an entire region and at randomly selected points within remnants patches of vegetation (ranging from 14.5 hectares to ~1426 hectares), where mistletoe numbers are generally lower. The level of mistletoe occurrence demonstrated in the current study, therefore, is comparatively high.

Although box mistletoe was more frequently seen on pink gums, logistic regression modelling demonstrated that the probability of mistletoe presence was roughly equal between pink gum, blue gum and box eucalypt *woodlands* (as opposed to individual trees). This indicates that the processes involved in an initial mistletoe occurrence developing into a proliferation (when a large percentage of trees are infected), occur in pink gum woodlands but not in other woodland types. Consequently, woodland type was identified as being more influential in determining mistletoe prevalence than more commonly discussed factors such as fragmentation and edge effects (Norton et al., 1995; Lavorel et al., 1999; Lopez de Buen et al., 2002). It is probable that

fragmentation and edge effects have, in fact, contributed significantly to the spread of box mistletoe on pink gums in the past. However, the current highly fragmented state of remnant vegetation in the MLR and the high mistletoe abundances have probably made discerning fragmentation and edge effects, at this late stage in time, impossible.

6.2. *Pink gum woodland, tree condition and box mistletoe prevalence*

In a conservation sense, the most alarming result of the present study was the poor condition of the pink gums that were surveyed. 51 % of all pink gums demonstrated evidence of considerable dieback and on average 48 % of the canopy of pink gums had senesced.

Although it is difficult to compare these figures against other studies of eucalypt health (because of different survey techniques), a quick comparison of results and methodologies gives an idea of the state of pink gums within the study area. For example, surveys by land managers on the Eyre Peninsula of South Australia indicated that as many as 50 % of the remaining River Red Gums *E. camaldulensis* showed severe signs of dieback (Paton et al., 2000b). Also, Paton and Eldridge (1994b) found that reconnaissance survey of the health of tree in different settings in the South East and 81 % of sites surveyed in the South East of South Australia contained eucalypts exhibiting some signs of ill health or dieback. However, dieback was most severe amongst scattered trees and there were *negligible* signs of dieback in remnant woodlands (Paton and Eldridge, 1994b). Again, given that the present study focused only on tree condition within remnant woodlands, the condition of pink gums and the outlook for their long term preservation can be described as dire.

6.3. *Individual tree features and box mistletoe prevalence*

The comparisons between the architectures of host and non-host pink gums, and their surrounding environments (see Table 5), are generally consistent with patterns of mistletoe occurrence on individual trees in Australia (Lamont, 1985b; Reid, 1988; Reid et al., 1992; Norton et al., 1995; Downey et al., 1997; Jameson, 1997) and overseas (Donohue, 1995b; Norton et al., 1997; Bannister and Strong, 2001b; Lekunze and Hassan, 2001; Lopez de Buen et al., 2002). Generally, those pink gums more likely to host box mistletoe were larger, more voluminous, were closer to infested conspecifics but had more isolated canopies. Also modelling indicated that

the height of the tree and the degree of canopy cover immediately surrounding the tree were the most influential factors determining mistletoe prevalence.

Taller, more voluminous trees are more likely to host mistletoe primarily for two reasons: 1) they are older, and have therefore been exposed to mistletoe colonisation for a longer period, increasing the probability of successful mistletoe establishment; and 2) older trees have a greater abundance of smaller twigs, and therefore have a greater abundance of potential perches for dispersers, seed deposition and therefore germination and establishment.

The amount of canopy cover immediately surrounding pink gums is likely to influence the prevalence of mistletoe primarily because of disperser behaviour. The main disperser of mistletoe in the Mount Lofty Ranges, the mistletoebird, is well known to be a direct flier (pers. obs, Heumann, 1926; Cheke et al., 2001) which, after visiting a tree, moves rapidly and directly to another tree, sometimes a considerable distance away. Because of such behaviour, individual trees whose canopy is not physically or visually obscured by surrounding canopies, are going to receive visits from mistletoebirds. Further to this, taller trees, which are more likely to 'stick out' above the surrounding canopy layer, are therefore more likely to receive visits from mistletoebirds, and subsequently host mistletoe.

6.4. Is the poor condition of pink gums a result of high mistletoe abundance?

A comparison of the amount of canopy dieback between box mistletoe host and non-host trees indicates that on average 57 % of the canopy of host trees has senesced, while on average 41 % of the canopy of non-host trees has senesced. Although no significance test was placed on these figures, I would be hesitant to implicate box mistletoe on the overall poor condition of pink gums, given that pink gums without mistletoe have such high default levels of dieback. Furthermore the levels of epicormic growth were very similar, and logistic regression modelling indicated that there was little relationship between the level of dieback and the presence or absence of box mistletoe.

Therefore, although it is possible that the extra stress of hosting high levels of mistletoe raises the average level of dieback, the default health of pink gums, with or

without a mistletoe infestation, is very poor. It is probable, therefore, that high mistletoe infestations are more likely to be symptomatic of the poor tree condition rather than causal.

An alternative hypothesis of why pink gum condition is poor may involve upheavals in groundwater regimes. At two of the reserves where surveys were carried out, Sandy Creek and Aldinga Scrub, there have been significant changes in groundwater regimes through abstraction of groundwater for sand mining and diversion of water for agricultural purposes. In addition, pink gum condition is poor at both sites. It is known that such groundwater abstraction and water diversions for mining, agriculture and urban development can have a considerable negative impact on terrestrial vegetation condition (Groom et al., 2000; Sinclair Knight Merz, 2001; Murray et al., 2003) Given that these areas are not known to be widely affected by other potential causes of dieback (e.g. root pathogens) and there were no signs of insect induced leaf mortality, it is possible that pink gum woodlands are phreatophytic, or Groundwater Dependent Ecosystems (GDE, Hatton and Evans, 1998b; Sinclair Knight Merz, 2001). Given the dire condition of pink gums demonstrated in this study, further investigations are urgently required to confirm whether pink gums are a GDE so that suitable groundwater regimes can be allocated in the future.

6.5. Why is mistletoe abundance so high on pink gums?

The high abundance of box mistletoe in pink gum woodlands in the MLR is likely to result from an accumulative effect of changes in a number of factors which regulate mistletoe abundance (Norton and Reid, 1997).

Firstly, it is possible that box mistletoe germination and establishment is greater on stressed hosts than non-stressed host. Yan and Reid (1995) indicated that box mistletoe establishment rates may be higher in trees whose canopy allows greater penetration of light. This is probably because for most mistletoe species, light, even at low intensities, increases percentage germination by up to four times (Lamont, 1983). The canopy dieback seen on stressed pink gums, therefore, would lead to higher irradiance in these canopies and higher germination and establishment rates of box mistletoe. Consequently, the large scale dieback of pink gums may have led to higher abundances of mistletoe on pink gums than on other eucalypt types. To assess this

possibility, however, an investigation into germination and establishment rates on stressed and non-stressed pink gums is required.

Furthermore, post-dispersal predation by rosella parrots (*Platycercus* spp.) is known to be a major cause of early mistletoe seedling mortality (Yan and Reid, 1995). It was noted during the study that the remaining pink gum woodlands in the MLR do not provide vast amounts of hollow bearing trees, and therefore rosella parrots are not common (author's obs). Therefore, the predation pressures of rosellas may be reduced in pink gum woodlands, leading to higher mistletoe abundances. It is difficult to implicate the high levels of mistletoe occurrence on large scale declines in brush-tailed possum numbers or large scale fire suppression (Norton and Reid, 1997), however. This is because there are locations in the study area, such as Sandy Creek, where both mistletoe and possum numbers are high, and fire has not disproportionately been absent from pink gums woodlands (author's obs.).

Lastly, it is conceivable that the architecture of individual pink gums and their immediate environment make pink gum woodlands more susceptible to the effective dispersal of mistletoe than individual trees in other eucalypt woodlands. Modelling of mistletoe prevalence on individual trees indicated that box mistletoe was more likely to be present on trees with less canopy cover immediately surrounding its canopy. The primary disperser of mistletoe in the MLR, the mistletoebird, moves directly and rapidly between trees (pers. obs, Heumann, 1926; Cheke et al., 2001). Therefore more 'open' woodlands, and individual trees whose canopy is not physically or visually obscured by surrounding canopies, are more likely to be more attractive and therefore receive more visits from mistletoebirds.

Thus mistletoe dispersal may be more effective in pink gum dominated woodlands because they are more open than other woodlands, and the large scale dieback of pink gum canopies demonstrated in this study may have enhanced this effect. In essence, the dieback may have led to an increase in the amount of 'edge' within remnant pink gum woodlands, thereby increasing the accessibility for mistletoebirds within the woodland, attractiveness of individual trees for perching, and therefore efficiency and effectiveness of mistletoe dispersal.

7. Conclusions

The explanations given in this report for the poor condition of pink gums, and for the high mistletoe abundances on Pink Gums, are presently only speculative, and assume a detailed and comprehensive understanding of the influences of tree condition on mistletoe germination and establishment (e.g. Yan and Reid, 1995), as well as disperser movements and behaviour (e.g. Reid, 1984, 1989; Monteiro et al., 1992; Martinez et al., 1995; Aukema and Martinez del Rio, 2002). In order to better understand the drivers of higher mistletoe abundance in pink gum woodlands of the MLR, therefore, further examination of box mistletoe germination rates and Mistletoebird movement and foraging behaviour is required.

The present study has, however, provided a framework for these future investigations and has highlighted the dire condition of Pink Gums in the MLR and an urgent need for further investigation into the importance of groundwater to these woodlands. It has also given a comprehensive description of mistletoe abundance and the drivers of mistletoe prevalence in the fragmented and degraded eucalyptus woodlands of the MLR.

8. Acknowledgments

Funding for the project was provided primarily by the Native Vegetation Council (S.A.) and the University of Adelaide. Additional funds were supplied by the Nature Conservation Society. Permission to work in the National Parks and Conservation Parks of the Mount Lofty Ranges. Mapping information was provided by Department for Water, Land and Biodiversity (S.A.).

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10. Manuscript

Determinants of Box Mistletoe *Amyema miquelii* occurrence and host condition in *Eucalyptus* woodlands of the Mount Lofty Ranges, South Australia.

Matthew J. Ward

School of Earth and Environmental Sciences, University of Adelaide, North Terrace, Adelaide, S.A.
5005, Australia.

Abstract

Mistletoe occurrence, host condition and habitat variables were measured at 89 sites across the Mount Lofty Ranges, South Australia, to investigate the influence of landscape features and tree architecture on box mistletoe *Amyema miquelii* prevalence (presence / absence) in *Eucalyptus* woodlands. Data were analysed using an information – theoretic approach, GIS and descriptive statistics. Logistic regression and model ranking using Akaike’s Information Criteria (AIC) indicated that woodland type was the most influential factor on mistletoe prevalence across the landscape. 28 % of all pink gums *E. fasciculosa* across the study area hosted box mistletoe. The condition of pink gums was poor for both host (58 % canopy dieback) and non-host (41 %) trees, indicating that the high levels of mistletoe occurrence is probably symptomatic rather than causal of poor tree condition. Logistic regression indicated individual trees with less foliage cover surrounding their canopy were more likely to host box mistletoe. Given these results, I propose that high mistletoe abundances in pink gum woodlands primarily results from the accumulative effect of high germination and establishment rates and enhanced conditions for seed dispersal by Mistletoebirds *Dicaeum hirundinaceum*, and these effects may have been enhanced by extensive canopy dieback. Further investigations into germination and establishment rates of box mistletoe and the behaviour of Mistletoebirds in these woodlands are required to assess these possibilities.

Keywords:

Box Mistletoe *Amyema miquelii*; Pink Gum *Eucalyptus fasciculosa*; canopy dieback; mistletoe proliferation, Information - theoretic approach; Akaike's Information Criterion; Logistic regression; Geographical Information System.

Introduction

Mistletoes from the family Loranthaceae are arboreal, hemi-parasitic flowering plants which produce their own photosynthetic products, but which depend on the xylem sap of their host to provide water and mineral nutrients (Calder and Bernhardt, 1983; Ehleringer and Marshall, 1995; Watling and Press, 2001). They are dependent on birds for the direct dispersal of seeds to suitable locations on the small branches of host plant species, and the distribution of mistletoes across a landscape is therefore strongly dependent on disperser foraging behaviour and movements (Reid, 1989, 1990, 1991; Martinez et al., 1996; Lopez de Buen and Ornelas, 2001). The prevalence and abundance of mistletoes is also regulated by a range of abiotic and other biotic factors (Norton and Reid, 1997), which can act at differing spatial scales (Aukema, 2004).

At a landscape scale, mistletoe presence and abundance may be restricted by the distribution and abundance of suitable host species, dispersers and pollinators (Norton and Reid, 1997). Habitat fragmentation can lead to an increase in mistletoe abundance within remaining vegetation patches (Lavorel et al., 1999), while in contrast canopy fires and widespread herbivory are likely to control and potentially decrease mistletoe abundances (Kelly et al., 1997). Variations in soil type (Bunderson et al., 1986), habitat quality (Hawksworth, 1961; Lei, 1999) and topographical features such as elevation, steepness of slope and aspect (Hawksworth, 1961, 1968; Smith, 1972; Ganguly and Kumar, 1976; Merrill et al., 1987; Aukema, 2004) are all potential influences on mistletoe distribution and abundance.

The abundance of mistletoe on individual trees generally increases with tree height, diameter and basal area (Donohue, 1995a; Downey et al., 1997; Bannister and Strong, 2001a; Lopez de Buen et al., 2002), and trees closer to an 'edge' or an infested conspecific are more likely to host mistletoe (Norton and Stafford Smith, 1999; Lopez de Buen et al., 2002). The establishment success of juvenile mistletoes is influenced by the branch diameter on which it is deposited (Reid, 1989; Sargent, 1995), as well as physical factors such as the nutrient and water status of the individual host (Reid, 1988; Norton and Reid, 1997), canopy light regimes, tree density (Lamont, 1983; Norton et al., 1997; Sweetapple et al., 2002) and potentially genetic compatibility (Reid et al., 1995). Furthermore the preferential perching and feeding of specialist mistletoe dispersers in previously infected host trees produces dramatic patterns of high mistletoe abundance on individual trees (Monteiro et al., 1992; Martinez et al., 1995; Larson, 1996; Aukema and Martinez del Rio, 2002; Aukema, 2004).

In the fragmented woodlands of south-eastern Australia, box mistletoe *Amyema miquelii* occurs on a wide range of *Eucalyptus* species (Barlow, 1992; Downey, 1997). Since the early 1900s, there has been numerous reports of damagingly high levels of mistletoe infestation in these parts of rural Australia, particularly of box mistletoe (Reid and Yan, 1995). It is generally accepted that these proliferations have occurred as a result of changes to a series of environmental filters which act to regulate mistletoe distribution and abundance, including host specificity, pollination, dispersal, habitat quality, predation and disturbance events (Norton and Reid, 1997).

Although box mistletoe proliferations have often been linked to rural tree decline, the link is not straightforward and proliferations may often be symptomatic rather than the cause of tree decline (Reid et al., 1992). For example Reid *et al.* (1994) demonstrated that the impact of box mistletoe on eucalypt survival and growth varied considerably between host species, and there are many cases of rural tree decline which do not involve mistletoe but rather changes in hydrology (Yates et al., 2000), insect attack (Landsberg and Wylie, 1983) or pathogens (Paton et al., 2000a; Reid and Landsberg, 2000). Therefore more detailed investigations of the factors driving mistletoe abundance in particular landscapes are required. There are also calls for such studies from communities who are concerned about tree decline and perceived high mistletoe abundances.

Epidemiology of box mistletoe proliferations, however, is difficult because of the wide and interrelated range of regulating factors, and the fact that the primary drivers of mistletoe proliferations are likely to vary at differing spatial scales (Aukema, 2004). In order to provide better resolution of epidemiological patterns, this study investigates mistletoe abundances and tree health in temperate *Eucalyptus* woodlands of the Mount Lofty Ranges, South Australia, at a landscape and an individual tree scale. Specifically, the study objectives were to: 1) quantify the extent of mistletoe occurrence on different eucalypt types in the Mount Lofty Ranges; 2) investigate the relationship between mistletoe prevalence with tree condition for the primary host of box mistletoe in the study area (pink gum *Eucalyptus fasciculosa*); and 3) examine how landscape features and individual tree characteristic influence box mistletoe prevalence (presence / absence) for a range of woodland types and for individual trees.

Methods

Study site

The study was carried out in the southern Mount Lofty Ranges (MLR) of South Australia (138° 42' 28" E, 34° 58' 34" S). The climate is temperate, with temperatures in winter and summer averaging 11° C and 20° C respectively. Mean annual rainfall varies from 400 - 1100 mm, with most precipitation occurring in the winter months (Laut et al., 1975). Vegetation of the MLR is primarily eucalypt woodland, particularly *Eucalyptus baxteri*, *E. obliqua*, *E. fasciculosa*, *E. leucoxylon* and *E. viminalis*. More than 90% of native vegetation cover has been cleared (Bryan, 2000; Paton et al., 2000a), with eucalypt woodlands in lower elevation areas of the MLR having been disproportionately cleared due to greater agricultural suitability (Paton et al., 2000a). As a result, much of the remnant vegetation patches and reserves of the MLR are highly fragmented and occur on poor quality land. There are a total of about 4000 native woodland patches in the MLR, with an average size of 13.1 ha (Westphal et al., 2003).

Study structure / site selection

In order to investigate the determinants of box mistletoe occurrence at different scales and to investigate the relationship between mistletoe prevalence and tree condition, a three - tiered study was carried out of eucalypt woodlands at a landscape and individual tree scale between July and November 2003.

The study was confined to National Parks and Conservation Parks ('reserves' herein) of the MLR (Fig. 1). Using ArcView 3.2 (ESRI, 1999), 30 reserves were partitioned with a 500 m x 500 m theoretical grid. Study sites in each reserve were then selected by randomly choosing up to six points where the 500 m x 500 m grid lines intersected. Hence the minimum distance between any two study plots was 500 m, minimising any spatial autocorrelation. Some potential sites were not used because of inaccessibility, and several supplementary sites were chosen so that a representative portion of all major woodland types was covered. 89 sites were selected in total. The vegetation associations covered by all study sites is given in Appendix 1.

Landscape features - box mistletoe prevalence

To investigate which broad landscape features influence box mistletoe prevalence at a landscape scale, a 20 m wide x 200 m long transect running east to west was walked at each of the 89 study sites. Within this transect, box mistletoe abundance was assessed by counting the number of live and dead box mistletoes on each eucalypt, and the species of eucalypt was recorded. This was carried out until either 50 trees had been surveyed, or the observer had walked 200 m west from the transect start point. Landscape features recorded for each transect location included woodland type, topography, dominant soil type, distance to the nearest edge and fragmentation.

Woodland type (WT) was determined from the dominant eucalypt within each transect's vegetation association (see Appendix 1) and classified as either: blue gum (*E. leucoxylon*); red gum (*E.*

camaldulensis); pink gum (*E. fasciculosa*); box eucalypt (*E. microcarpa*, *E. odorata*, *E. goniocalyx* and *E. porosa*); manna gum (*E. viminalis* subsp. *cygnetensis* and *E. viminalis* subsp. *viminalis*); or stringybark (*E. obliqua* and *E. baxteri*) woodland. Other landscape features were classified using a GIS in Arcview 3.2 (ESRI, 1999). Topography (TOPO) was classified in the field as either gentle, slope, valley / creek or hill top / ridge and later confirmed using a digital elevation map of the MLR (Bryan, 2003). A solar radiation index (RAD) was obtained from a physical environmental model linked to a GIS (Bryan, 2003), and used as an alternative representation of topography, on the premise that the amount of solar radiation received at a site is a function of location, slope, aspect and topographic shading at a particular site. Soil type (SOIL) was categorised from a GIS soil map of the region (see Appendix 2 for categories, PIRSA, 2001). Distance to edge (EDGE) was defined as the distance from the middle of the transect to the nearest edge of the remnant vegetation patch, and was calculated from a vegetation map. Fragmentation (FRAG) was recorded by creating theoretical buffers (300 metres radius) around the middle of each transect, and calculating the Mean Shape Index for the vegetation within these buffer zones using Patch Analyst (Elkie et al., 1999), an extension in ArcView. Mean Shape Index equals one when the buffer patch consists of an unbroken circular patch of vegetation, and increases infinitely as the vegetation patch shape becomes more fragmented and irregular (McGarigal and McComb, 1995).

Tree condition - box mistletoe prevalence

In order to investigate the relationship between tree condition and the prevalence of box mistletoe, extra information was recorded for study sites which were located in pink gum woodlands, including 1) the condition of the box mistletoe on individual trees; 2) the extent of canopy dieback on each pink gum; and 3) the level of epicormic growth of each pink gum. The condition of box mistletoes on each tree was scored as either: the majority of mistletoes on a pink gum unhealthy (discoloured and demonstrating signs of dieback); some mistletoes unhealthy, some healthy (little foliage discolouration or dieback); or the majority of mistletoes healthy. Canopy dieback of individual trees was determined by visibly assessing what proportion of the canopy was still intact and what proportion had senesced. For example if 80% of the volume of foliage of the tree was still intact, a score of 20 % was recorded. Those trees with at least 40 % canopy dieback were considered to be demonstrating significant levels of canopy dieback. Eucalypt trees that are stressed will often produce epicormic shoots along their branches or trunk. The level of epicormic growth was therefore recorded as the percentage of total foliage present on the plant that was being provided by recent epicormic shoots and branchlets.

Individual tree features - box mistletoe prevalence

To determine which individual tree characteristics influence the prevalence of box mistletoe on individual pink gums, a detailed study was made of host and non-host pink gums at 17 study sites where box mistletoe was abundant (five sites at Sandy Creek, one at Cromer, six at Onkaparinga River, four at Aldinga Scrub and one at Anstey's Hill Conservation Parks, Fig. 1). Transects that had previously been used for landscape and pink gum woodland health surveys were divided into five 20 m wide x 40 m long cells (Fig. 2). At the beginning and in the middle of each cell (10 m either side), the

closest pink gum > 3 m in height (host or non-host) was chosen as the first survey tree (Fig. 2). Following this, the closest pink gum within the same cell and at least 5 m away from the previously surveyed tree was chosen as the second survey tree (Fig. 2). If the first tree surveyed within a cell was a host tree, the second tree chosen (also > 3 m in height) was a non-host pink gum, and vice versa. If there was no host or no non-host pink gums within one of the 20 m x 40 m cell, then only one pink gum was recorded for that cell.

On each pink gum the presence / absence of live and dead box mistletoe were recorded. Tree characteristics recorded included: diameter at breast height (DBH), height (HEIGHT), height of lowest canopy, canopy area, canopy volume (CA.VOL), relative height difference (RHD) between the pink gum and surrounding vegetation, surrounding canopy cover (COVER), dieback (DIEBACK), distance to the nearest mistletoe infested eucalypt (NRST.MTOE) and the number of live and dead box mistletoe within 5 m of the canopy cover. In addition the horizontal (inner or outer) and vertical (lower, mid or outer) distribution of each mistletoe within the pink gum canopy was recorded.

DBH was measured using a ruler and the height of each pink gum was measured using a clinometer. Canopy area was determined by measuring the canopy radius in four cardinal directions from the base of the tree of each pink gum, and using the formula for the area of a circle (Πr^2). Canopy volume (CA.VOL) was determined by measuring the height of the lowest canopy with a clinometer, comparing this with the total height of the tree and using the formula for the volume of a sphere ($4/3\Pi r^3$). These measurements were also used to describe the crown (canopy) depth ratio (CDR) and crown shape ratio (CSR, Tanabe et al., 2001). CDR is the ratio of the height of the canopy (tree height minus height of lowest canopy) : height of the tree. A smaller CDR indicates a shallower canopy. CSR is the ratio of canopy height : crown radius (average of canopy radius in 4 directions). The smaller the CSR is, the more planar the canopy.

Both RHD and COVER were determined by taking recordings at 1 m, 3 m and 5 m out from the edge of the canopy of each tree in four cardinal directions, so that a total of 12 recordings were made per tree for each measurement (Fig. 3). Relative height difference was recorded by estimating the height to within half a metre (relative to the pink gum) of the tallest vegetation within a 1 m radius around each measuring point (Fig. 3). For example if an adjacent pink gum was approximately one metre smaller than the recorded pink gum, a recording of minus one was made. An average relative height difference was given for the 12 recordings taken for each tree. COVER was measured by looking vertically through a 55 mm long x 50 mm diameter cylinder divided into 4 quarters, counting the number of quarters (0 - 4) in which foliage (above 3 m in height) was present, and expressing the total count (between 0 and 48 for all 12 measurements around each pink gum) as percent cover.

Data analyses

An information-theoretic approach was used to investigate the relationship between landscape and individual tree features and mistletoe prevalence (Burnham and Anderson, 2002). Landscape (WT,

TOPO, EDGE, SOIL and FRAG) and individual tree features (HEIGHT, COVER, CSR, NRST.MTOE, CA.VOL and DIEBACK) were used as explanatory variables in the a priori development of a set of 15 and 18 models of mistletoe prevalence (presence / absence response variable) at a landscape and individual tree scale respectively. These model sets included global models with all explanatory variables. Interactions among the variables were not considered. Not all tree characteristics were used as explanatory variables in models of mistletoe prevalence for individual trees because some were autocorrelated (e.g. HEIGHT and DBH). Models were fitted using generalized linear modelling (GLM) assuming a binomial error structure (1= mistletoe presence, 0 = mistletoe absence) with a logit link function (logistic regression) using S-PLUS 6.1 (Insightful, 2002).

Candidate models were ranked using Akaike's Information Criterion (AIC, Burnham and Anderson, 2001, 2002). This information – theoretic approach uses Kullback - Leibler information (Kullback and Leibler, 1951) to objectively identify, from the a priori candidate set, the best fit model, which explains the most substantial proportion of variance in the data, yet is parsimonious and does not include unnecessary parameters that cannot be justified given the data (Burnham and Anderson, 2001, 2002). For all candidate models in the present study, model selection was based on a second – order bias corrected form of AIC (AICc) because n / K (sample size / number of parameters) was less than 40 (17.8 and 25 for the models of mistletoe prevalence at a landscape and individual tree scale respectively).

Candidate models were ranked by evaluating the difference (Δ_i) between the AICc for model i and the minimum AICc (Table 2). The larger the Δ_i , the less likely that model is the K-L best model in the set of candidate models being considered, given the data, and models having $\Delta_i \leq 2$ have substantial empirical support as candidate models (Burnham and Anderson, 2001, 2002). The plausibility of each model was also ranked using $\Lambda(g_i|x)$, the likelihood of model g_i , given the data, as well as Akaike weights (w_i). Akaike weights can be considered as the probability of model i being the actual K-L best model given the set of candidate models being considered (Burnham and Anderson, 2001, 2002).

Descriptive statistics are also given for aspects of the data, including the frequency and abundance of mistletoe on different *Eucalyptus* species, the condition of pink gums relative to mistletoe prevalence, and the individual features of host and non-host pink gums.

Results

Landscape features - box mistletoe prevalence

A total of 4221 individual eucalypt trees, representing 11 different species, were measured for box mistletoe prevalence across the MLR (Table 1). Across all species, 12.6% of all trees measured hosted live box mistletoe, and these 523 host trees had on average 2.7 ± 0.1 (mean \pm s.e.) live box mistletoe per tree.

Pink gums had a greater number of individual trees hosting a greater number box mistletoe than other eucalypt species, with 28.5% of all pink gums surveyed hosting at least one live box mistletoe, and almost 10% and 5% hosting greater than three and five live box mistletoes respectively (Table 1). In comparison, 10.9%, 3.4% and 1.7% of all blue gum *E. leucoxylon* hosted at least one, three and five live box mistletoe respectively, followed by box eucalypt species *E. microcarpa*, *E. odorata* and *E. porosa* (5.3%, 1.3% and 0.9%), cup gum *E. cosmophylla* (4.3%, 0.6% and 0%) and red gum *E. camaldulensis* (2.2%, 0.7% and 0.2%). The percentages of other eucalypt species (long-leaved box *E. goniocalyx*, stringybark *E. baxteri* and *E. obliqua*, and manna gum *E. viminalis*) infested with at least one live box mistletoe were $< 1\%$ (Table 1). Box mistletoe occurrence rates on host trees (mean \pm s.e.) were similar between pink gum and blue gum (both 2.7 live mistletoe per tree), however comparisons between other eucalypt species does not hold significant meaning because of the small number of host trees. (Table 1).

From the logistic regression analyses, AICc model selection criteria indicated that woodland type (WT) was found to be the best fit model, having a 58% probability of being the best model of box mistletoe prevalence from the candidate set (as indicated by the Akaike weight, w_i , Table 2, Burnham and Anderson, 2002). The next best model of box mistletoe presence / absence was a combination of woodland type and fragmentation ($w_i = 0.36$). All other models were comparatively unlikely ($w_i \leq 0.02$). According to Burnham and Anderson (2002), inferences should only be based on models that make up the top 90% of Akaike weights. In this case, the top two models fit this criterion and both models included woodland type (WT) as a parameter (Table 2). Hence, these top two models indicate that box mistletoe prevalence varied strongly depending on woodland type. Given the large difference in Akaike weights and the similar parameterisation of these models, model-averaging procedures were not required. Probability estimates from the best model (WT) indicated that for the area encompassed within transects at each study site, there was roughly equal probability ($\approx 80\%$) of mistletoe being present in blue gum, box eucalypt and pink gum woodlands (as opposed to individual trees), which decreased for red gum (50%), manna gum ($\approx 17\%$) and stringybark woodlands ($\approx 15\%$, Table 3).

Tree condition - box mistletoe prevalence

Of the 1200 pink gums surveyed, 31.9% hosted live box mistletoe, while almost 38% hosted live or dead box mistletoe (Table 4). On average there were 0.89 live and 0.15 dead mistletoes per tree for all trees measured, and on pink gums there was an average of 2.79 live mistletoes and 0.59 dead mistletoes

per tree. Of all pink gums measured, 44.3, 39.1 and 16.6% had primarily healthy, healthy and sick, and primarily unhealthy box mistletoe respectively. The mean level of canopy dieback for all trees was 48%, and 52% of all pink gums had at least 40% (“substantial”) canopy dieback. Host pink gums had 58% canopy dieback (64.5% with substantial dieback) which increased to 43% for non-host pink gums (45.7% with substantial dieback). Mean epicormic growth for both host and non-host pink gums was 39%.

Individual tree features - box mistletoe prevalence

A total of 175 individual pink gums (95 host and 80 non-host) were surveyed in order to understand the features of host and non-host pink gums. For host trees, the majority of mistletoes occurred in the outer and upper portion of the canopy (79.8 and 46.52 % respectively, Fig. 4). Descriptive statistics for host and non-host pink gums are given in Table 5. Compared to non-host pink gums, host pink gums were on average: slightly taller (6.8 m for host c.f. 5.6 m for non host); had larger girth (DBH = 13.6 c.f. 10.3 cm), canopy area (30 c.f. 9.6 m²) and canopy volume (93.1 c.f. 23.6 m³); were more planar in shape (CSR = 1.5 and 2.9 for host and non-host pink gums); and had slightly greater levels of canopy dieback (48.3 c.f. 43.3 %). On average, canopy cover surrounding host trees (21.7 %) was less than for non-host trees (29.4 %), and host trees generally were taller relative to the surrounding vegetation (+ 2.96 m) than non-host trees (+0.97 m). Infested conspecifics were generally further away for non-host pink gums (9.8 m) than for host pink gums (7.0 m), and on average there were more mistletoes within 5 m of the host pink gums canopies (4.2) than for non-host pink gums (1.9).

Logistic regression analyses and model ranking indicated that COVER was the best model, having a 34 % probability (as indicated by Akaike weights) of being the best model for box mistletoe prevalence in individual pink gums from the candidate set (Table 6). The other candidate models with reasonable support were HEIGHT ($w_i = 0.2$), followed by a combination of COVER and NRST.MISTLETOE ($w_i = 0.14$). Although the top three models indicated a degree of model uncertainty with Akaike weights < 0.4, model averaging was thought unnecessary because of the similar and parsimonious nature of those models which made up the top 90 % of Akaike weights. Those models which made up the top 90 % of Akaike weights all only contained two parameters, including either COVER and HEIGHT. Box mistletoe prevalence on individual pink gums, therefore, was primarily influenced by variations in the degree of foliage cover within 5 metres of the canopy of individual trees, and on the height of the tree.

Discussion

Across the Mount Lofty Ranges, box mistletoe prevalence was primarily influenced by woodland type, with the highest probability of mistletoe presence in pink gum, blue gum and box eucalypt woodlands (all members of the *Adnataria* section of the *Symphomyrtus* sub genus, Nicolle, 1997). However, the frequency of individual trees hosting a greater number of box mistletoe was far higher on pink gums than all other eucalypt species, with 28% of pink gums hosting at least one box mistletoe, and 5% hosting at least five box mistletoes.

Despite low host specificity across its range (Barlow, 1984; Downey, 1997), the higher frequency and abundance of box mistletoe on particular eucalypt types, as demonstrated for pink gums in the present study, is not atypical (Lamont, 1985a; Reid et al., 1994; Yan and Reid, 1995; Downey et al., 1997; Fagg, 1997). Similar levels of mistletoe occurrence have been demonstrated in previous studies (Lamont, 1985a; Reid and Yan, 1995). Yet these studies focused on scattered trees and narrow vegetation corridors, where mistletoe abundances are generally higher. In comparison, the present study was conducted across an entire region at randomly selected points within remnant patches of vegetation, where edge and fragmentation effects, which can be key drivers of increases in mistletoe abundance (Norton et al., 1995; Lavorel et al., 1999; Lopez de Buen et al., 2002), should theoretically be minimised. This indicates that the levels of mistletoe occurrence on pink gums demonstrated in the present study can be considered particularly high, which may also have made identification of fragmentation and edge induced mistletoe prevalence difficult to identify.

The other outstanding result from the present study was the poor condition of the pink gums that were surveyed. 52 % of all pink gums demonstrated evidence of considerable dieback and on average 48 % of the canopy of pink gums had senesced. Given that similar levels of dieback of Eucalypts in south-eastern Australia are more often seen on scattered trees in agricultural settings (Paton and Eldridge, 1994a; Paton et al., 2000a), the condition of pink gums within the remnant patches of vegetation across the MLR can be considered very poor. Two interesting questions arise from these results in regards to mistletoe. First, is the poor condition of pink gums a result of the high mistletoe abundance? Second, why is mistletoe abundance so high on pink gums?

A comparison of the amount of canopy dieback between box mistletoe host and non-host trees indicates that on average 57 % and 41 % of the canopy had senesced on host and non-host trees respectively. Given that both host and non-host pink gums are in such poor condition, it is unlikely that mistletoe is the cause of the high levels of dieback recorded in this study. Furthermore, the levels of epicormic growth were similar, and logistic regression modelling indicated that there was little relationship between the level of dieback and the prevalence of box mistletoe. Therefore, although it is possible that the extra stress of hosting mistletoe can increase canopy dieback, the general health of host and non-host pink gums is poor, and high mistletoe abundance is possibly symptomatic of the poor tree condition rather than causal.

In the MLR, pink gums are not known to be widely affected by other causes of dieback such as root pathogens or insect induced leaf mortality. A credible alternative hypothesis for poor pink gum condition is that pink gum woodlands are phreatophytic (groundwater dependent) ecosystems, and their poor condition has resulted from the significant changes in hydrology that have occurred over much of the MLR. This is often cited as a cause of deterioration in terrestrial vegetation condition in rural areas of Australia (e.g. Hatton and Evans, 1998a; Groom et al., 2000; Sinclair Knight Merz, 2001; Murray et al., 2003).

If the high mistletoe abundances in pink gum woodlands is symptomatic of the poor condition of pink gums rather than causal, why do pink gum woodlands support high mistletoe abundances? Given that there was a roughly equal chance of mistletoe presence in pink gum, blue gum and box eucalypt woodlands, pink gum woodlands per se are not more susceptible to initial occurrence of mistletoe. However the greater frequency and abundance of box mistletoe indicates that pink gum woodlands are more conducive to the conditions that allow mistletoe occurrence to progress from relatively normal levels to high abundances. This has probably resulted from the accumulative effect of a number of changes in the factors which regulate mistletoe abundance (Norton and Reid, 1997), particularly dispersal and habitat quality.

For example, the architecture of individual pink gums and their immediate environment, particularly in their current poor condition, may make pink gum woodlands more susceptible to the effective dispersal of mistletoe. Modelling of mistletoe prevalence on individual trees indicated that box mistletoe was more likely to be present on trees with less canopy cover immediately surrounding its canopy. While this may suggest that mistletoes prefer the higher irradiance that would result from lower canopy cover, mature mistletoes (including *Amyema*) have the photosynthetic characteristics of shade plants (Strong et al., 2000; Matsubara et al., 2001). Therefore, the greater prevalence of mistletoe on the outer parts of the canopy of trees with little surrounding canopy cover is more likely to result from disperser behaviour and, paradoxically, more suitable light conditions for the establishment of *juvenile* mistletoes (see below, Lamont, 1983; Yan and Reid, 1995).

The primary disperser of mistletoe in the MLR, the mistletoebird, moves directly and rapidly between trees (author's obs., Heumann, 1926; Cheke et al., 2001). Therefore more 'open' woodlands, and individual trees whose canopy is not physically or visually obscured by surrounding canopies, are likely to be more attractive and therefore receive more visits from mistletoebirds. Thus mistletoe dispersal may be more effective in pink gum dominated woodlands because they are more open than other woodlands, and the large scale dieback of pink gum canopies demonstrated in this study may have enhanced this effect. In essence, the dieback may have led to an increase in the amount of 'edge' within remnant pink gum woodlands, thereby increasing the accessibility and attractiveness of trees for mistletoebirds within the woodland, and therefore the efficiency and effectiveness of mistletoe dispersal.

It is also possible that the dieback of pink gum canopies has produced a better quality microhabitats for the germination and establishment rates of box mistletoe. This is because for most mistletoe species, light can increase germination percentage by up to four times (Lamont, 1983), and Yan and Reid (1995) indicated eucalypt canopy structure and light penetration was an important factor in the establishment rates of box mistletoe. The canopy dieback of stressed pink gums seen in this study, therefore, could have led to higher irradiance within pink gum canopies, and subsequently higher establishment rates of box mistletoe. To assess this possibility, however, an investigation into germination and establishment rates on stressed and non-stressed pink gums is required.

The establishment and abundance of mistletoes in Australia is also restricted by fire (Kelly et al., 1997; Norton and Reid, 1997; Reid, 1997) and herbivory by brush-tail possums (*Trichosurus vulpecular*) (Reid, 1997) and rosella parrots (*Platycercus* spp.) (Yan and Reid, 1995). To assess the impacts of fire, further investigation is required to determine the relative frequency of canopy fires in different woodland types. However, the large difference in mistletoe abundances between eucalypt types, and a general lack of canopy fires in the MLR for at least 20 years, suggests processes such as high germination rates contribute more significantly to the relatively higher mistletoe abundances on pink gums. Furthermore, although possums are relatively common in the MLR, it is difficult to ascertain their effect on mistletoe abundance, because they may more often seek alternative food sources (Reid, 1997). The influence of rosella predation may have some significance, however, as recent bird surveys in the MLR indicated rosella absences were generally correlated with pink gum dominated woodlands (S. Field, unpublished data). This suggests the post dispersal mortality of box mistletoes, through herbivory by rosella parrots (Yan and Reid, 1995), would be lower in pink gums woodlands.

The numerous explanations given here are presently only speculative, however, and in part assume a comprehensive understanding of box mistletoe establishment (e.g. Yan and Reid, 1995), as well as disperser movements and behaviour (e.g. Reid, 1984, 1989; Monteiro et al., 1992; Martinez et al., 1995; Aukema and Martinez del Rio, 2002). In order to better understand the drivers of mistletoe proliferations in pink gum woodlands of the MLR, therefore, further examination of box mistletoe germination rates and mistletoebird behaviour are required. However, the present study has provided a framework for future investigations, a perspective into the dispersal and management of mistletoe in pink gums woodlands of the MLR, and an indication of the drivers of mistletoe prevalence in fragmented and degraded eucalyptus woodlands.

Acknowledgments

The study was inspired by the concerns of David Paton for tree condition in South Australia. Funding for the project was provided by the Native Vegetation Council (S.A.), Nature Conservation Society of South Australia and a University of Adelaide Faculty of Science Postgraduate Scholarship. The Department of Environment and Heritage (S.A.) provided permission to work in the National Parks and Conservation Parks of the Mount Lofty Ranges and digital vegetation maps for the Mount Lofty Ranges. Digital soil and elevation maps of the MLR were supplied by Brett Bryan, GISCA, University of Adelaide. Wendy Telfer and David Wilson took brief relief from the tropics to provide company during field work. David Paton and Wendy Telfer read and improved earlier drafts of the manuscript.

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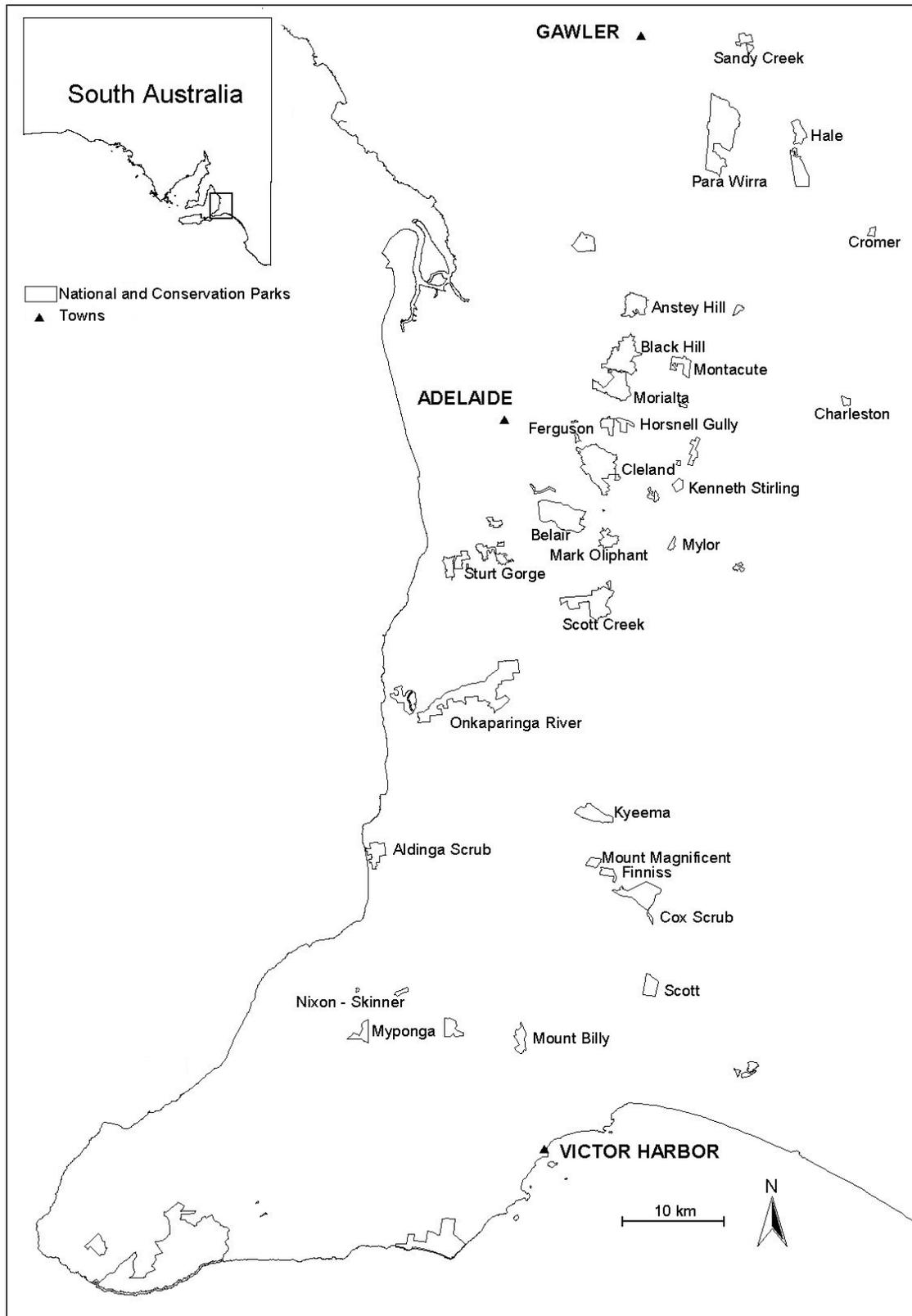


Figure 1. National and Conservation Parks in which landscape features – *Amyema miquelii* box mistletoe occurrence and *Eucalyptus fasciculosa* pink gum condition studies were conducted. The individual tree – box mistletoe study was conducted in Sandy Creek, Cromer, Onkaparinga River and Aldinga Scrub Conservation Parks.

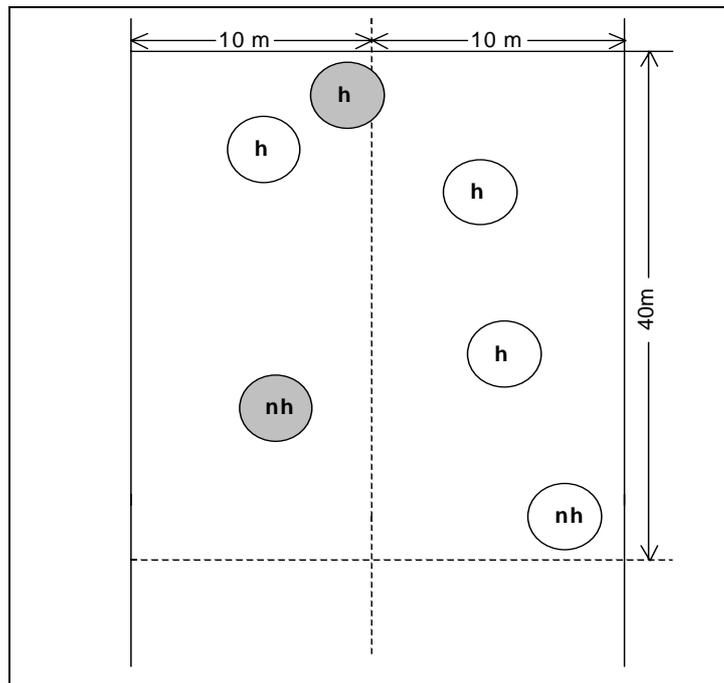


Figure 2. Example of a transect cell used in the survey of individual *E. fasciculosa* pink gum / *Amyema miquelii* box mistletoe study. Circles represent pink gums, 'h' = host pink gum and 'nh' = non host. Shaded circles are those pink gums that would have been chosen to be surveyed. In this study, 20 m x 200 m transects were divided into five 20 m wide x 40 m long cells. The closest tree to the centre line of the cell was initially measured, followed by the closest (but at least 5 m apart) host or non-host pink gum, depending on whether the initial tree measured was a host or non-host pink gum. If the first tree measured was a host tree, then the second tree chosen to be measured would have been a non-host tree, and vice versa. If there was either no host or no non-host pink gums within the 20 m x 40 m cell, then only one pink gum was measured. Therefore, a maximum of 5 host and 5 non-host pink gums were measured per transect.

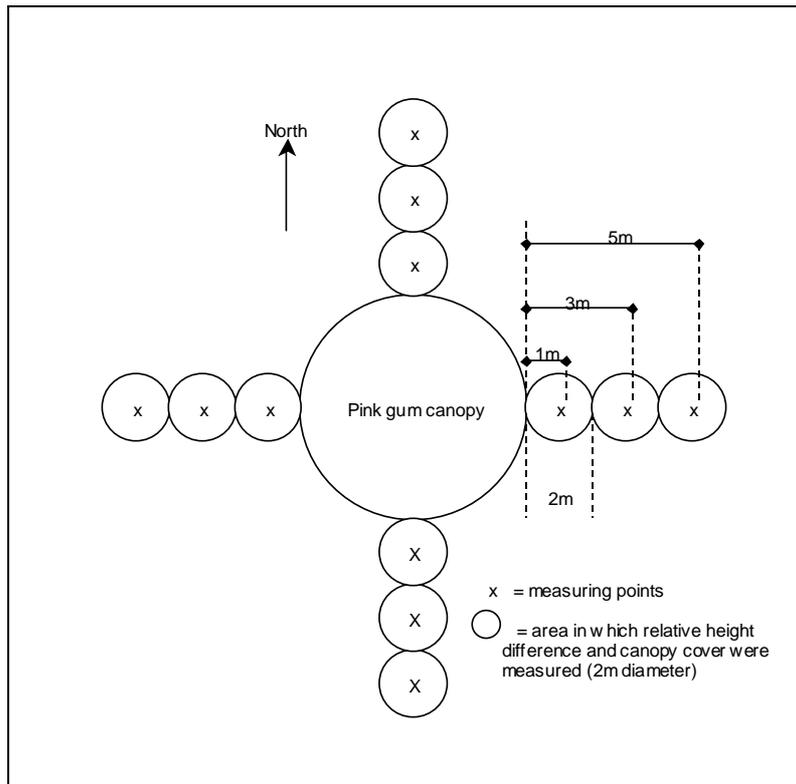


Figure 3. Sampling design for surrounding canopy cover (COVER) and relative height difference (RHD) between individual *E. fasciculosa* pink gums and the surrounding vegetation, as measured in the individual pink gum / *Amyema miquelii*-box mistletoe study. Measuring points were located 1 m, 3 m and 5 m out from the canopy of each pink gum in a north, east, south and west direction. RHD was recorded as the relative height (to within 0.5 m), compared to the height of the pink gum, of the tallest vegetation falling within a 1 m radius of each measuring point. The 12 recordings made for each pink gum were summed to give a total RHD of the surrounding vegetation. COVER was measured by looking vertically through a 55 mm long x 50 mm diameter cylinder divided into 4 quarters and counting the number of quarters (0-4) in which foliage was present, and expressing the total of 12 readings around each tree as percent cover.

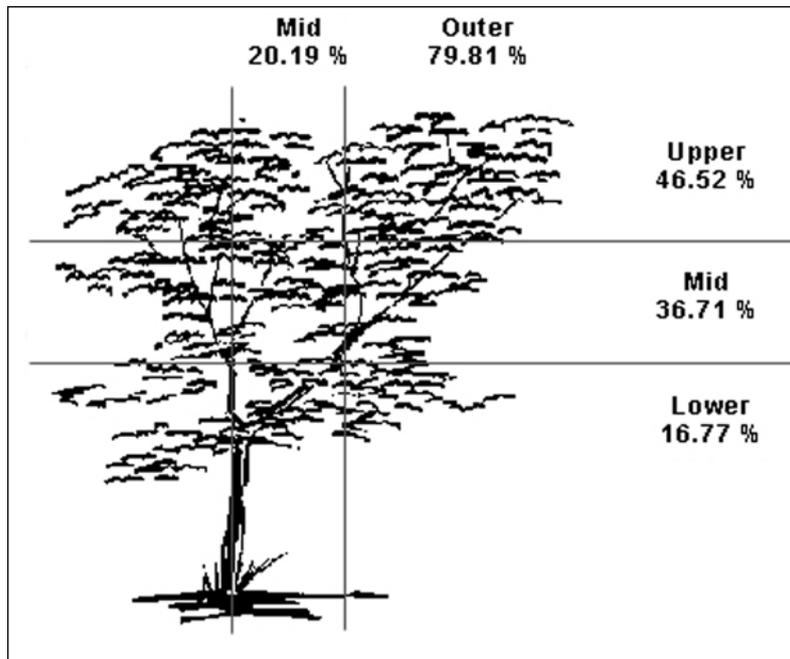


Figure 4. Diagrammatic representation of the percent of live *Amyema miquelii* box mistletoe distributed in different parts of *Eucalyptus fasciculosa* pink gum canopies in the Mount Lofty Ranges, South Australia.

Table 1. Summary statistics of landscape features - box mistletoe *Amyema miquelii* study. n = the total number of each *Eucalyptus* species examined for box mistletoe. ‘Box eucalypts’ *E. microcarpa*, *E. odorata* and *E. porosa* (all members of the Adnataria section of the Symphomyrtus sub genus, Nicolle, 1997) and ‘stringybark’ eucalypts (*E. obliqua* and *E. baxteri*) were combined to provide more meaningful statistics. Given is the % of each tree species which hosted at least one, two, three, four or five box mistletoe, as well as the mean number of box mistletoe per tree for host trees only. N/A indicates there were insufficient host trees (< 10) for meaningful statistics.

<i>Eucalyptus</i> species	n	% of trees hosting <i>x</i> live <i>A. miquelii</i>			# <i>A. miquelii</i> per host tree mean \pm s.e. (n)
		$x \geq 1$	$x \geq 3$	$x \geq 5$	
<i>E. fasciculosa</i>	1494	28.5	9.9	4.7	2.7 \pm 0.1 (425)
<i>E. leucoxylon</i>	643	10.9	3.4	1.7	2.7 \pm 0.4 (70)
<i>E. microcarpa</i> / <i>E. odorata</i> / <i>E. porosa</i>	228	5.3	1.3	0.9	2.3 \pm 0.9 (13)
<i>E. cosmophylla</i>	163	4.3	0.6	0	N/A (7)
<i>E. camaldulensis</i>	465	2.2	0.7	0.2	2.9 \pm 1.3 (10)
<i>E. viminalis</i>	232	0.4	0	0	N/A (1)
<i>E. baxteri</i> / <i>E. obliqua</i>	764	0.3	0	0	N/A (2)
<i>E. goniocalyx</i>	232	0.9	0	0	N/A (2)
Total (4221)	4221	12.6	4.2	2.0	2.7 \pm 0.1 (530)

Table 2 Results of logistic regression analyses of box mistletoe presence / absence in the southern Mount Lofty Ranges. Explanatory variables in candidate models are, WT = woodland type, FRAG = fragmentation index, EDGE = distance to the nearest edge, TOPO = topography, RAD = solar radiation index and SOIL = dominant soil type. Δ_i = the difference between that model's second order bias corrected form of Akaike's Information Criteria (AICc), and the minimum AICc value. $\Lambda(g_i|x)$ = the likelihood of model g_i , given the data, and w_i = Akaike weights. Candidate models with significant levels of empirical support ($\Delta_i < 2$) are shown in **bold**.

Candidate model	Δ_i	$\Lambda(g_i x)$	w_i
1. WT	0.00	1.00	0.54
2. WT + FRAG	0.87	0.65	0.35
3. WT + RAD	4.56	0.10	0.06
4. WT + FRAG + EDGE	6.85	0.03	0.02
5. WT + EDGE	7.70	0.02	0.01
6. EDGE	8.30	0.02	0.01
7. FRAG	9.62	0.01	< 0.001
8. FRAG + EDGE	9.63	0.01	< 0.001
9. RAD	10.31	0.01	< 0.001
10. TOPO	21.41	< 0.001	< 0.001
11. WT + TOPO + RAD	21.75	< 0.001	< 0.001
12. TOPO + RAD	23.78	< 0.001	< 0.001
13. TOPO + EDGE	23.89	< 0.001	< 0.001
14. TOPO + FRAG + EDGE	24.53	< 0.001	< 0.001
15. FRAG + TOPO + RAD	24.92	< 0.001	< 0.001
16. WT + TOPO	25.84	< 0.001	< 0.001
17. SOIL + TOPO + RAD	30.61	< 0.001	< 0.001
18. WT + SOIL	44.13	< 0.001	< 0.001
19. SOIL	44.41	< 0.001	< 0.001
20. GLOBAL	141.83	< 0.001	< 0.001

Table 3 Probability of mistletoe presence in different *Eucalyptus* woodlands, based on the best fit model of mistletoe prevalence as determined by logistic regression analysis and model ranking with AIC.

Woodland type	Probability of mistletoe presence (%)
Blue Gum	81.8
Pink Gum	78.1
Box Eucalypt	77.8
Red Gum	50.0
Manna Gum	16.7
Stringybark	12.5

Table 4. Summary statistics of pink gum *Eucalyptus fasciculosa* woodland and box mistletoe *Amyema miquelii* survey. ‘Canopy dieback’ represents an estimation of the percentage of the potential canopy that is no longer present as a result of dieback. ‘Epicormic growth’ was estimated as that percentage of the present canopy that is made up of recent epicormic growth. A ‘host *E. fasciculosa* is classified as a Pink Gum with a live mistletoe on it.

Measurement	Non – host	Host	All
	<i>E. fasciculosa</i> (n = 817)	<i>E. fasciculosa</i> (n = 383)	<i>E. fasciculosa</i> (n = 1200)
% of <i>E. fasciculosa</i> hosting live <i>Amyema miquelii</i>	-	-	31.9
% of <i>E. fasciculosa</i> hosting live or dead <i>A. miquelii</i>	-	-	37.8
# live <i>A. miquelii</i> per <i>E. fasciculosa</i> (mean ± s.e.)	-	2.8 ± 0.2	0.9 ± 0.1
# dead <i>A. miquelii</i> per <i>E. fasciculosa</i> (mean ± s.e.)	-	0.6 ± 0.1	0.2 ± 0.0
% <i>E. fasciculosa</i> with primarily healthy box mistletoe	-	44.3	
% <i>E. fasciculosa</i> with healthy and unhealthy box mistletoe	-	39.1	
% <i>E. fasciculosa</i> with primarily unhealthy box mistletoe	-	16.6	
% canopy dieback (mean ± s.e.)	43.3 ± 1.3	57.7 ± 1.7	47.9 ± 1.1
% epicormic growth (mean ± s.e.)	38.5 ± 1.5	39.4 ± 2.0	38.8 ± 1.2
% <i>E. fasciculosa</i> with at least 40 % canopy dieback	45.7	64.5	51.7

Table 5. Summary statistics of individual pink gum *Eucalyptus fasciculosa* / box mistletoe *Amyema miquelii* survey. ‘tree’ refers to *E. fasciculosa*, and ‘mistletoe’ refers to box mistletoe. ‘Host *E. fasciculosa*’ is a pink gum hosting a live box mistletoe.

Measurement	Host <i>E. fasciculosa</i> (mean ± s.e)	Non-host <i>E. fasciculosa</i> (mean ± s.e.)
# trees surveyed (n)	95	80
Number of live mistletoe / tree	3.5 ± 0.4	N/A
Number of dead mistletoe	0.9 ± 0.2	N/A
Height (m)	6.8 ± 0.2	5.6 ± 0.2
DBH (Diameter at breast height, cm)	13.6 ± 0.6	10.3 ± 0.5
Canopy area (m ²)	29.9 ± 3.7	9.6 ± 1.6
Canopy volume (m ³)	93.1 ± 14.3	23.6 ± 5.3
CDR (Crown depth ratio)	0.5 ± 0.02	0.6 ± 0.02
CSR (Crown shape ratio)	1.5 ± 0.1	2.9 ± 0.4
% canopy dieback	48.3 ± 3.3	43.3 ± 4.1
Surrounding Canopy Cover (%)	21.7 ± 1.2	29.4 ± 1.1
Relative height difference between tree and surrounding vegetation (m)	+ 3.0 ± 0.2	+ 1.0 ± 0.2
Distance to nearest mistletoe infested tree (m)	7.0 ± 0.7	9.8 ± 1.3
Average # mistletoe within 5m of Pink Gum Canopy	4.2 ± 0.6	1.9 ± 0.3

Table 6. Results of logistic regression analyses of individual pink gum *Eucalyptus fasciculosa* / box mistletoe *Amyema miquelii* survey conducted in October – November, 2003, in the Mount Lofty Ranges, South Australia. Explanatory variables in candidate models are: HEIGHT = height; CSR = canopy shape ratio; COVER = surrounding canopy cover; CA.VOL = canopy volume; NRST.3m = distance to nearest tree > 3m in height; DIEBACK = canopy dieback. Δ_i = the difference between that model's second order bias corrected form of Akaike's Information Criteria (AICc), and the minimum AICc value. $\Lambda(g_i|x)$ = the likelihood of model g_i , given the data, and w_i = Akaike weights. Candidate models with significant levels of empirical support ($\Delta_i < 2$) are shown in **bold**.

Candidate model	Δ_i	$\Lambda(g_i x)$	w_i
1. COVER	0	1.00	0.34
2. HEIGHT	0.96	0.62	0.21
3. COVER+NRST.MTOE	1.86	0.40	0.13
4. HEIGHT+NRST.MTOE	2.08	0.35	0.12
5. COVER+DIEBACK	2.20	0.33	0.11
6. HEIGHT+DIEBACK	3.141	0.21	0.07
7. HEIGHT+COVER	6.43	0.04	0.01
8. DIEBACK	9.36	0.01	< 0.001
9. NRST.MTOE	9.37	0.01	< 0.001
10. CSR	23.31	< 0.001	< 0.001
11. COVER+CSR	23.52	< 0.001	< 0.001
12. HEIGHT+CA.VOL	26.44	< 0.001	< 0.001
13. CSR+NRST.MTOE	26.46	< 0.001	< 0.001
14. CSR+DIEBACK	27.85	< 0.001	< 0.001
15. COVER+CA.VOL	33.85	< 0.001	< 0.001
16. CA.VOL	33.91	< 0.001	< 0.001
17. GLOBAL	76.35	< 0.001	< 0.001